THE PHYSIOLOGICAL ECOLOGY OF

CLEMATIS VITALBA L.

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Frontspiece. Clematis vitalba in flower.

CONTENTS

Chapter Page

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

ABSTRACT

The object of the investigation was to determine factors influencing the distribution of C. vitalba in New Zealand, and to distinguish areas which may be susceptible to infestation.

Seed of C. vitalba required exposure to light for germination. Exposure 5 min/day to light resulted in significantly higher total germination than long exposure (16 hr photoperiod).

Transplantation of C. vitalba seedlings into different forest types showed a strong correlation between survival and percentage of total photosynthetically active photon flux density (PPFD) received. Gas exchange measurements demonstrated a high PPFD saturation level for stomatal conductance and assimilation. Stomatal opening took 20 minutes to complete after transfer from shade to high PPFD. Shading of plants grown in a glasshouse experiment resulted in significantly less growth at light intensities of less than 14% of full sunlight.

C. vitalba grew significantly faster on soil from a podocarp forest than on soil from a beech forest. Addition of phosphorus to the beech forest soil significantly increased growth but there was no response to added calcium. Seedlings of C. vitalba grew best in well drained soil. Waterlogged soil significantly reduced growth. The major factor influencing distribution of C. vitalba is soil drainage rather than a calcium requirement.

Therefore C. vitalba is a light demanding plant which can establish only in relatively open sites. Podocarp forests south of Auckland on free-draining sites are extremely susceptible to invasion due to the high fertility of the soils under this forest type.

Herbicide-soaked wooden plugs, inserted into mature stems, proved to be a safe and effective control method.

CHAPTER 1

INTRODUCTION

Clematis vitalba, a polycarpic perennial woody vine, was initially introduced to New Zealand as an ornamental (Healy, 1969) and also as root stock for the establishment of scions of other Clematis species. Since its growth is vigorous and rapid, its escape from cultivation has resulted in heavy infestations in forests. Damage to native bush has resulted from smothering by C. vitalba, particularly in lowland and coastal areas.

C. vitalba is known by a number of common names (Table 1.1). The most frequently used are Old Man's Beard due to the fluffy grey seed heads (Sowerby & Sowerby, 1899), and Traveller's Joy because it provided a pleasant scented shade for travellers (Gerard, 1597).

1.1 DESCRIPTION

Clematis vitalba, is a member of the Ranunculaceae which originates in Western Europe. It is a deciduous woody climber which may grow to heights of up to 30 metres (Mitchell, 1975).

Seedlings are small rosette plants with opposite, simple, ovate, serrate leaves. When conditions are favourable, internodes will elongate and compound leaves are produced. The first compound leaves produced have three leaflets increasing to the five leaflets commonly found on mature plants.

Leaves on adult plants are pinnate usually with (3-)5 rather distant leaflets. Leaflets are 3-10cm long, narrowly ovate, acute or acuminate in shape. The leaf bases are rounded or subcordate and the margins are coarsely toothed or entire. Leaves are glabrous or slightly pubescent.

Traveller's Joy	Gerard (1597)	Provided pleasant scented shade for traveller's.
Viorna	Gerard (1597)	Classified as such by Lobel "Viorna, quasi vias ornans"
Vitis Alba	Gerard (1597)	"White vine" classified by Dodonaeus.
Old Man's Beard	Sowerby & Sowerby (1899)	Named for the fluffy grey seed heads.
Clematite blanche	Sowerby & Sowerby (1899)	French translation of the latin name.
Steigende Waldrebe	Sowerby & Sowerby (1899)	German translation of the latin name.
Virgins Bower	Mitchell(1975)	Several Clematis spp. with white flowers have this name.
Wild Clematis	Mitchell(1975)	?
Herbe aux gueux	Bean (1970)	"Begger's plant" Its acrid juice was used by beggers in Paris to produce ulcerous wounds as a means of exciting pity.
Smoke-wood or Smoking cane	Sowerby & Sowerby (1899)	Village boys smoked pieces of the wood as large vessels in wood allowed air to circulate freely.

Table 1.1 Common names of Clematis vitalba.

Long, simple hairs (Fig 1.1) and glandular hairs (Fig 1.2) are present on pubescent leaves.

Flowers are c. 2 cm in diameter, produced in terminal and axillary panicles and fragrant (Frontspiece). Flowers are usually hermaphroditic, actinomorphic, and hypogenous. There are usually 4 perianth segments which are petalliod, greenish-white in colour and densely pubescent outside. There are numerous staminodes and carpels. Achenes are found in large heads and are pubescent with long whitish plumose styles (Clapham et al., 1962). The seed and style at maturity form the dispersal unit.

Flowering occurs in Continental Europe from June to August (Polunin, 1969) and in Britain from July to occasionally as late as September (Mitchell, 1975).

Young stems have deep longitudinal ridges and furrows, and are dark purple on surfaces exposed to light and pale green in shaded stems. Older stems have a characteristic grey, loose, long, shredding bark. The nodes of young stems are thickened and are 15-18cm apart (Mitchell, 1975). Nodes on older stems become indistinguishable as diameter increases and may only be detected where there is root or shoot growth from the node (Fig 1.3).

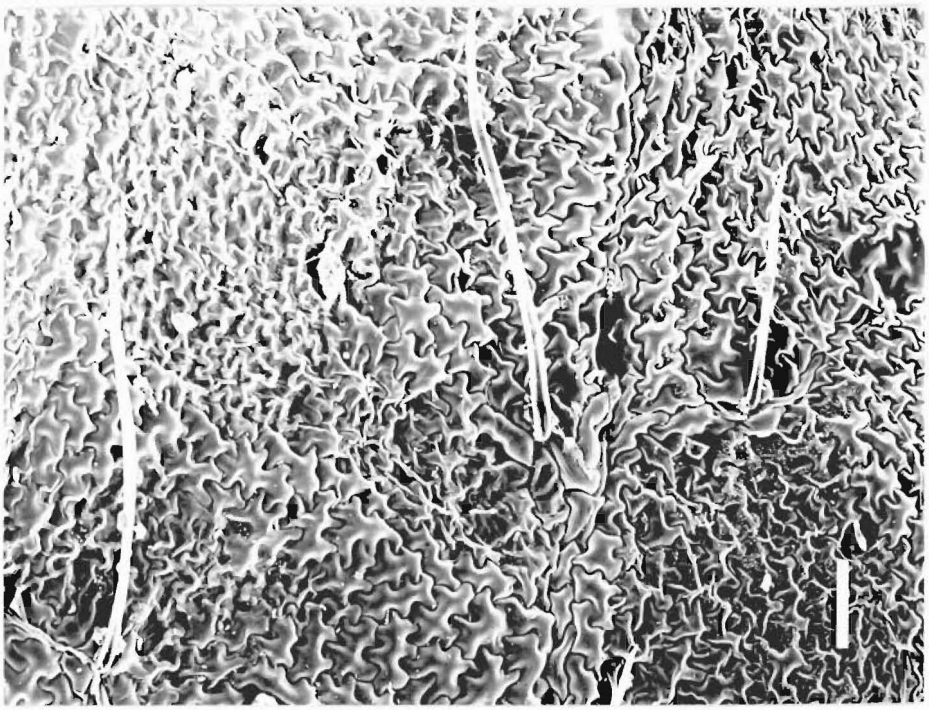


Fig 1.1 Scanning electron micrograph of hairs on leaf surface of C. vitalba (bar=100 µm).

Fig 1.2 Scanning electron micrograph of a glandular hair on the leaf surface of C. vitalba (bar=40 µm).

1.1.2 Growth Habit

Vines will grow either unsupported on the ground, over small shrubs, hedges and embankments or supported by large trees. Leaflet petioles twine around other plants as it grows towards the canopy. Stems are able to grow unsupported to approximately 1 metre in height. This enables them to reach low branches of small trees and shrubs. If support is not reached stems fall to the ground and and grow along the ground. Further upright shoots may be produced at nodes along the prostrate stem.

Once the canopy has been reached, a mass of stems will cover the tree canopy smothering the tree underneath. Stems will either drop back to the ground and root, eventually returning to the canopy, or pass from one tree canopy to another (Fig 1.4). Eventually supporting trees will die due to lack of light.

Flowers are produced only when the plant is growing in a position of high light interception, (on top of the tree canopy or on unshaded prostrate plants). This confers an advantage for wind dispersal of seeds. The growth habit of C. vitalba gives a high degree of exposure of the seeds to wind.

The ability of the leaflet petioles to twine is important in the success of this species. Darwin (1875) studied the sensitivity of the petiole in Clematis species including C. vitalba. He observed that rubbing the lower surface of young petioles induced a slight downward curvature. After 5 hrs the end of one was bent back parallel to the basal portion.

Fig 1.3 Young shoot sprouting from a mature vine which has rooted at the node.

Fig 1.4 C. vitalba growing on the forest canopy at the Goose Bay-Omihi Scenic Reserve.

1.2 DISTRIBUTION

1.2.1 European Distribution

C. vitalba is native to Britain (Mitchell, 1975) and South, West and Central Europe. It has been introduced to Ireland, Norway, Sweden and Poland (Tutin et al., 1964; Polunin, 1969).

In Britain its natural range extends north to Clywd and South Yorkshire (Mitchell, 1975). The presence of C. vitalba in the North of England, Scotland and Ireland is possibly due to its introduction to these areas (Sowerby & Sowerby, 1899).

In Europe it ranges north to Holland (Mitchell, 1975) and it is also found in North Africa and the Caucasus (Mitchell, 1975; Hansen, 1972). It has been naturalised in Denmark, where it was cultivated as an ornamental plant and became a garden escape (Hansen, 1972). Stands of C. vitalba in Poland along the Middle Vistula in the Kazimierz, Dolny and Janowiec region are considered to be of secondary or artificial origin (Boratynski, 1974).

1.2.2 New Zealand Distribution

The first published record of C. vitalba in New Zealand was by Allan (1940). C. vitalba was then listed as being present in a few localities in the North Island. It was not considered to have established sufficiently to have claim to naturalisation. Forty years later C. vitalba was included in a list of plants naturalised in New Zealand. Its distribution was listed as Auckland, Bay of Plenty, East Cape, Taranaki, Manawatu, Wairarapa, Wellington and the South Island except Westland (Garnock-Jones, 1981).

Atkinson (1982) gives more detailed distribution records for New Zealand but states that the records show an incomplete picture of the present distribution. Most of the records are taken from scenic reserves where the search has been most concentrated. The worst affected areas are in Central New Zealand (Atkinson, 1982).

1.3 FACTORS AFFECTING DISTRIBUTION

Atkinson (1982) suggested factors that may limit the further spread of C. vitalba. These include cool temperatures at higher altitudes, low rainfall, adverse soil physical conditions, low soil fertility particularly low base status, and dense shade.

1.3.1 Altitude and Latitude.

The distribution of C. vitalba according to latitudinal zones and altitudinal belts in Europe shows that it occurs mostly in warm climates and is in northern central Europe (Ellenberg, 1974). In New Zealand C. vitalba rarely occurs above 750 m. The predominantly lowland distribution suggests that growth of C. vitalba may be limited by cooler temperatures of higher altitudes (Atkinson, 1982).

1.3.2 Light.

Establishment of seedlings of C. vitalba does not occur readily in the shade. Infestations of the vine in native forest frequently begin at the forest edge or in canopy gaps. These canopy gaps can be the result of windfall, death of canopy trees or damage by slips (Atkinson, 1982). Ellenberg (1974) states the occurrence of C. vitalba in relation to relative light intensity during summer is that of a "1/2 light plant" rarely receiving less than 50% light.

1.3.3 Soil

Soil Water Content. In Europe C. vitalba occurs in aerobic soils or under intermediate soil moisture conditions (Ellenberg, (1974). On the middle Vistula in Poland C. vitalba usually occupies the drier and warmer places (Boratynski, 1974). According to Mitchell (1975) C. vitalba requires unimpeded drainage and a warm, loose structured soil.

Soil Fertility. C. vitalba is often associated with riverbeds with high frequency. Since alluvial soils often have a high fertility this suggests soil fertility is important. The other major soil classes on which C. vitalba is frequently found in New Zealand are:

1. Yellow-grey earths in 800-1000mm rainfall zone
2. Drier Central and Steepland Yellow-brown earths in the 1000-1600mm rainfall zone.

These soils commonly contain medium or high levels of calcium and other bases. The distribution of C. vitalba is at least partly associated with soils of moderate or high fertility (Atkinson, 1982). According to Ellenberg (1974) C. vitalba is mostly found in soils rich in mineral nitrogen.

Soil pH. C. vitalba occurs mostly in neutral soils, but also in acidic and basic ones (Ellenberg, 1974). In Britain C. vitalba is listed as a calcicole since it is commonly associated with chalk soils where calcium levels are high. It also occurs on a variety of soils especially those rich in bases (calcium, potassium, magnesium and sodium) (Salisbury, 1952). In the British Isles C. vitalba appears to be a calcicole, but tolerates a wider range of soils on the Continent, especially in more southerly regions. The influence of calcium carbonate status of the soils on growth seems to be subordinate to the soils' physical conditions (Sankey, 1966). Mitchell (1975) records C. vitalba as being abundant on alkaline soils with a requirement for a high base status.

Soil Type. In Britain C. vitalba is found mainly on calcareous soils (Sowerby & Sowerby, 1899) in shallow soils over chalk, and to a lesser extent over limestone. Requirements of unimpeded drainage and warm, loose structured soil, high base status and fertility, exclude it from most clays, sands and gravels (Mitchell, 1975).

In New Zealand C. vitalba is absent from the heavy clay soils north of Auckland. This suggests that growth of this vine may be restricted by the physical conditions of these yellow-brown earth soils. Two of the occurrences of C. vitalba in the Auckland locality are on Red and Brown loam soils. This class of soils in contrast to the yellow-brown earths, have good moisture-holding and aeration characteristics even though their chemical fertility is not high (Atkinson, 1982).

1.3.4 Rainfall

Atkinson (1982) suggested that C. vitalba may be limited by annual rainfalls lower than 800 mm. Its presence in the Clutha Valley where rainfall is lower than 800 mm contradicts this relationship with rainfall. However the old alluvial gold dredgings would allow roots to easily reach the water table. In other low rainfall areas, gullies, Seepages or other moist sites may still provide sufficient moisture for C. vitalba to establish.

1.3.5 Habitat

In Britain C. vitalba is found growing on hedgerows, scrublands, and on the edge of woodlands where the smothering effect is relatively unimportant. Physical blanketing by C. vitalba can be serious in young forestry plantations before the tree canopy closes (Mitchell, 1975).

In Denmark, where it is cultivated as an ornamental, it has escaped from gardens and is now naturalised. It has been recorded in a number of localities growing on slopes, in hedges, edges of woods and in railway areas (Hansen, 1972).

In Poland where it is also an introduced species, C. vitalba is associated with xerothermic communities of Peucedanum cervariae-Corylus woodland and more rarely in Festuca ovina grassland as well as on the edges of oak woodlands. It also occurs in hedges, on edges of orchards and in gardens (Boratynski, 1974).

In New Zealand C. vitalba occurs in a wide range of habitats including indigenous and artificial forests, coastal cliffs, gardens and in wasteplaces and untended land. It was introduced to New Zealand for ornamental horticulture and has since escaped (Healy, 1969). C. vitalba has become a troublesome weed in parts of New Zealand in patches of native forest and among deciduous trees. In the worst affected areas shading by the vine's foliage has resulted in the death of substantial areas of native forest (Atkinson, 1982).

The objective of this study was to gain more information on the ecology of Clematis vitalba. In

particular the effects of light, water and soil factors on germination, and establishment and growth of seedlings were studied. An understanding of the factors affecting the distribution of C. vitalba would distinguish susceptible areas.

(Nomenclature for native species follows Allan (1961) except for Pseudopanax.)

CHAPTER 2

PHENOLOGY

2.1 INTRODUCTION

There is relatively little information on the phenological development of C. vitalba in the literature. It is possible that under New Zealand conditions that it has a longer growing season than in Europe. A longer growing season might explain why it has become a serious weed problem. This study was to obtain further information on the development of C. vitalba. This information may be of future use in planning the timing of control measures to when the plant is at its most vulnerable stage.

Flowering in Continental Europe occurs from June to August (Polunin, 1969) and one month later in the British Isles (Mitchell, 1975). Fruits remain on the plant long after leaf fall (Bean, 1970). Fruits ripen from the end of September and practically all the achenes remain on the plant through winter. A high proportion can be found on the plants as late as the middle of May (Lhotska, 1973).

The only reference to flowering in New Zealand is from the Wanganui-Taihape area. In this area flowering occurs from December to March (Kennedy, 1980).

2.2 MATERIALS AND METHODS

2.2.1 Early Development

Observations were made of the developmental stages during seedling growth in the natural situation. These were noted as changes in relation to growth form and onset of flowering.

2.2.2 Phenology

At two Christchurch locations , part of 25 plants of C. vitalba were tagged. The sites chosen were:

1. Carlton Mill Rd and Bealy Ave corner.

   Plants growing on a fence along the bank of the Avon River upriver from Harper Ave Bridge.

2. Riccarton Rd and Hansons Lane corner.

   This site is an empty section surrounded by a high wooden fence on two sides. The fence is covered by vines of C. vitalba.

Using plastic tags, 15 plants were tagged at Site 1 and 10 at Site 2. Since it was impossible to identify individual plants of C. vitalba, areas of the vines were tagged at intervals along the fence on which they were growing. At the site of each tag a 1 metre wide area was observed and the percentage of the area in each phenological stage was estimated. Vegetative and floral stages were recorded separately. Each 1 m section is referred to here as a separate plant.

Vegetative Stages	
Bud Burst	Opening of the vegetative buds in the previous season's leaf axils.
Leaf Area Increment	Growth and expansion of leaves and stem.
Leaf area Increment Ceased	Period during which growth ceases and leaf senescence occurs.
Leaf Shedding	Abscission of leaves.
Leafless	Leaves shed and buds dormant

Table 2.1 Stages of Vegetative Development.

Reproductive Stages	
Flower Bud Formation	Time from bud formation in leaf axils to just before bud burst.
Flower Bud Burst	From when bud bursts till when stamens and styles exposed.
Flower Mature	From presentation of anthers to senescence of sepals.
Fruit Development	Swelling of seed.
Fruit Immature	Seed fully formed but still green.
Fruit Ripe	Fruit dry and brown.
Fruit Dispersed	Fruit released from receptacle.

Table 2.2 Stages of Reproductive Development.

Observations began in late May, and were made at two weekly intervals. In October one of the tagged plants at Carlton Mill Road was removed during maintenance by the Christchurch City Council. This reduced the number of plants at this site to 14. Herbicide was sprayed at the Church Corner site during early spring, to control weeds on the footpath over the fence. Early leaves were deformed but the plants phenology did not appear to be affected.

Measurement of seasonal biomass changes was attempted at the same sites. This was abandoned when stems selected for measurement were trimmed by Council workers during maintenance. These types of measurements need to be made at sites were human or animal disturbance is minimal. Due to the infrequency of visits to the Kaikoura field sites it was not possible to make these measurements at Kaikoura.

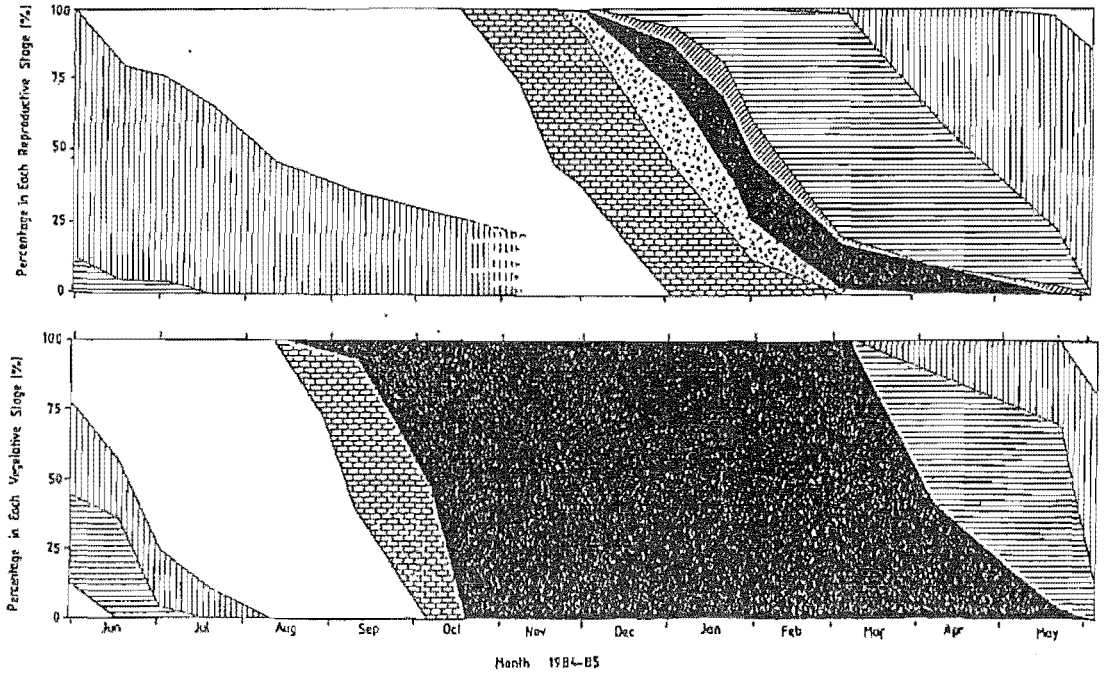
2.3 RESULTS

2.3.1 Early Development

Recently germinated C. vitalba seedlings were observed in October 1984 growing under the canopy of adult plants. After germination a small rosette plant is formed. The first leaves formed consist of a simple leaf; the second leaves are lobed and later leaves are divided into leaflets.

The plant remains in a rosette form until approximately 4 pairs of leaves are produced. If conditions are suitable the internodes lengthen and plants begin to climb or scramble over other plants.

Flowering has been observed to occur only when the plant reaches the canopy. Only parts of the plant exposed to full light will flower. The time to reach the canopy is variable and depends on conditions of the site. Plants grown in ideal conditions in the glasshouse flowered 12 months after germination.



Key

- Fruit Formation
- Fruit Immature Increment Ceased
- Fruit Ripe Leaf Shedding
- Fruit Dispersed Leafless
- Floral Bud Formation Bud Burst
- Floral Bud Burst
- Flowers Open Leaf Area Increment

2.1 Vegetative and reproductive phenological development of C. vitalba for the year June 1984 to May 1985.

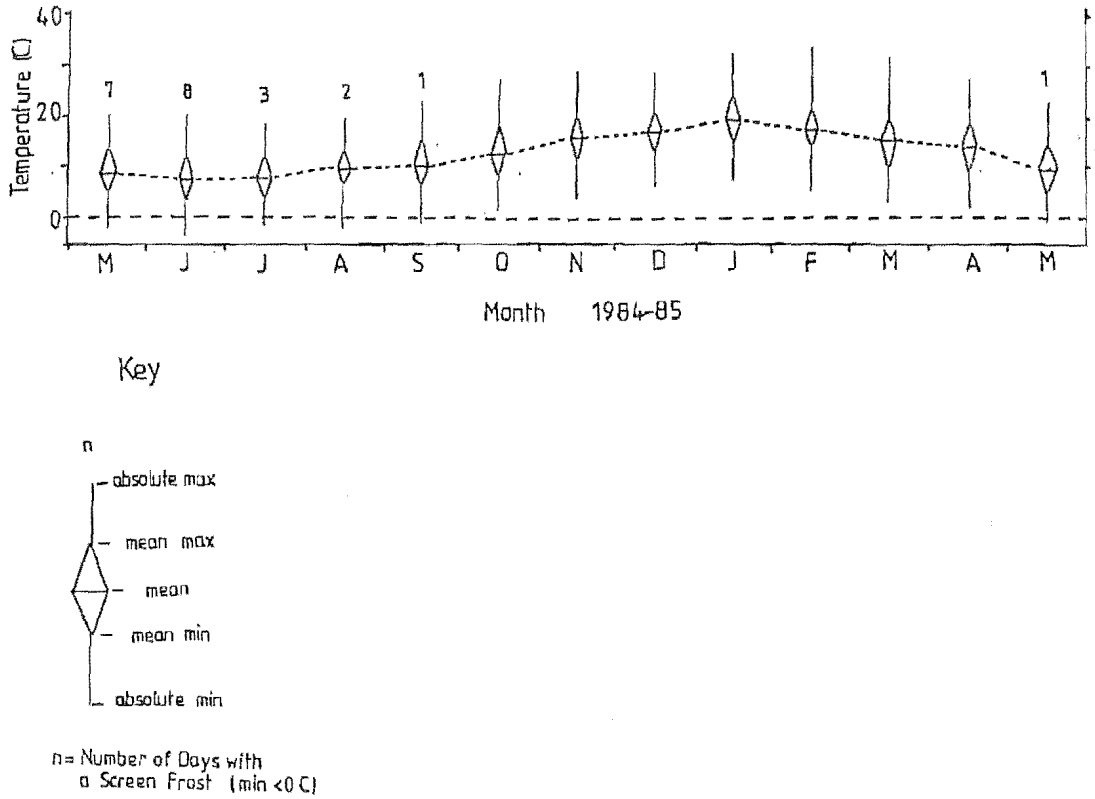


Fig 2.2 Monthly temperature for the period May 1984 to May 1985.

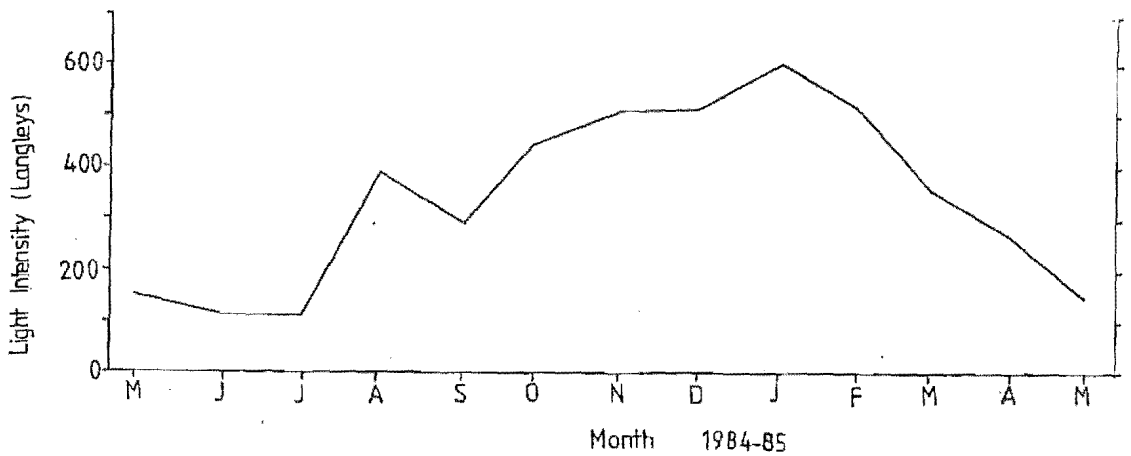


Fig 2.3. Monthly light intensity (Langleys) for the period May 1984 to May 1985.

2.3.2 Phenology

The phenological observations were graphed as percentages of plants in each phase of development, for the year June 1984 to June 1985 (Fig 2.1). Climate data for this period from the Christchurch Botanic Gardens has been supplied by the N.Z. Meteorological Service (Fig 2.2 and 2.3). The Carlton Mill Road site is 1 km, and the Church Corner site 4 km from the Botanic Gardens.

Vegetative Phenology. Vegetative buds in the previous seasons' leaf axils remain dormant over winter. Bud burst occurs in early August but vines remain almost leafless until early September when the growth phase of stem and leaf area increment begins. This phase continues until early May.

Leaf senescence begins mid-May but some leaves remain green until mid-June. Once senescence has occurred, abscission is rapid except in vines sheltered from wind. Vines remain leafless from early July till early September.

Floral Phenology. Floral buds form, approximately 2 months after vegetative buds burst, in early November in the leaf axils of the new seasons' growth. Flowering begins with bud burst in early December. The majority of flowering is over by early March but some flowering occurs up till early May. Late flowering does not result in fruit set. Seeds remain green until late in April when they darken to dark red-brown in colour and become dry.

Some fruit dispersal occurs in June and July but most fruit remains attached to the receptacle until August. Approximately 30% of the fruit appears to not be released, its dispersal is prevented by the growth of the new seasons' foliage.

Germination of seeds is rapid after dispersal. Seedlings were found growing in the litter around the adult vine in early September. These seedlings did not survive after the leaf expansion of the adult reduced light transmission.

2.4 DISCUSSION

2.4.1 Early Development

The total time for a C. vitalba seedling to develop to flowering depends on the site of establishment. Glasshouse results indicate that if conditions for growth are favourable it may only take a year before it will flower for the first time. Observations suggest that favourable conditions are related to either light intensity or light quality received.

2.4.2 Phenology

Leaf bud burst occurred in early August when the mean temperature was 9 C (Fig 2.1 and 2.2). At this time the risk of frost damage was still high. Most other exotic tree species originating from the British Isles and Europe were still leafless. Early bud burst would give vines of C. vitalba a chance of establishing before canopy trees blocked out light. Measurements of stem length increment were not obtained. However the rate of increment appeared to slow before flowering started in December.

Flowering appears to be associated with the light intensity received. Not only does the plant require to be fully exposed to light before it flowers but peak flowering is associated with the highest light intensities (Fig 2.3). It should also be noted that mean temperature and daylength, also peak at this time.

Fruit set and seed ripening are most likely to be affected by temperature. As the mean temperature decreased the amount of fruit setting was reduced. The absence of pollinators due to colder temperatures may also have been a factor in reducing fruit set.

Seed produced early in the season remained green until late April when they darkened. This darkening process coincided with the first frosts (Fig 2.2). Seed colour continued to darken over-winter. Germination experiments showed that the paler coloured seed, collected early in winter would not germinate. A period of chilling on the plant is required before germination will occur (Chapter 3).

Fruit was not released from the plant until August.

In Christchurch its dispersal was rapid as release coincided with the onset of strong North westerly winds. Fruit that was not dispersed was soon covered by the new seasons' growth.

CHAPTER 3

SEED ECOLOGY

3.1 INTRODUCTION

Seeds have mechanisms which allow them to recognise particular aspects of the external environment. Germination is regulated in response to these environmental factors. The germination of seeds and early growth of seedlings represent periods of maximum vulnerability to physical changes in the environment. Selection favours environmental cuing mechanisms that decrease the probability of encountering unfavourable conditions after germination (Angevine and Chabot, 1979).

3.1.1 Classification

A classification of seeds based on internal morphology places C. vitalba in the group of seeds with basal embryos of rudimentary type (Martin, 1946).

3.1.2 Light

Previous work claimed that light was of little importance in the germination and establishment of C. vitalba.

McClelland (1979) found that in a LD light regime 62% of seeds germinated, while in complete darkness 83% germinated. From this it was concluded that light did not influence germination. The difference between total % germination was attributed to a decreased humidity level in the light trial. The dishes in the complete darkness trial were wrapped in foil and possibly less subject to drying out than those in the light.

Tucker (1978) in a 2 way experiment involving temperature and light found no differences in the rate of germination and total % germination in different light

regimes. The light treatments were: 8hr light and 16hr dark, wrapped in tin foil, constant light, and in a dark room.

3.1.3. Temperature

Lhotska (1974) found that seeds of C. vitalba given warm stratification of 18 to 20 C resulted in only single cases of germination, and then only in seeds collected from samples at later periods (late winter or early spring). Seeds which were stratified at 32 C did not germinate and seeds decayed within a short time. Cold stratification of seeds at 5-10 C resulted in the start of germination being retarded an average of 10 days in comparison with seeds stratified at 7-10 C.

Lhotska's (1974) results show cold stratification at 8-12 C then transfer to 25 C resulted in a faster onset of germination than those kept at 7-10 C. Total % germination was lower than that of seed in the 7-10 C treatment collected early in the winter. The difference in total % germination between these two treatments decreased in seeds collected later in the year.

Tucker(1978) found that alternating temperatures between 20 C and 30 C were more effective in giving high germination % than constant temperatures of 20 C.

3.1.4. After-ripening

Where the embryo of a species is morphologically immature and requires further development before the seed will germinate, this period of development is described as after-ripening. The gradual reduction in dormancy takes place only in seeds which have a low water content. This occurs in nature when seeds experience long periods in the dry condition (Beweley and Black, 1982).

Fruits of C. vitalba ripen from the end of September with practically all the achenes remaining on the mother plant through the winter "bradysporic" in the sense of Lhotska (1973). In spite of the fruits being well exposed to the wind a high percentage of fruits are found on plants in Europe as late as May (Lhotska, 1973).

Experiments confirmed that growth of embryos in

species with hemibradysporic to bradysporic dissemination takes place not only in the soil and during stratification but also directly on the mother plant. In seeds with a dry pericarp, after ripening of the embryos on the mother plant takes place in seeds with a dry pericarp. This occurs provided that temperature conditions are favorable, under the influence of absorption of atmospheric moisture. The degree of after-ripening of embryos in dry fruits depends on the quality and distribution of rainfall in various years and on the course, of temperatures during the swelling of seeds (Lhotska, 1974).

During normal after-ripening or artificial chilling an increase of growth-promoting hormones, such as gibberellins or cytokinins, is thought to overcome seed dormancy in some species (Kramer and Kozlowski, 1979). Dormancy in C. vitalba was broken by treatment with Gibberellic acid (GA_3) 10^{-4} M (Grime et al., 1981). The influence of chilling can be examined by treatment of seeds with a gibberellin inhibitor before chilling treatment. Gibberellin inhibitors include 2- chloroethyltrimethylammomnium chloride (CCC), AMO1618, and Phosfon D (Lang, 1970). If a gibberellin inhibitor was found to prevent germination of seeds, spraying of seeds while still on the vine might inhibit germination long enough to reduce seed viability.

3.1.5. Dispersal

In spite of the fact that C. vitalba is well adapted to wind dispersal and its growth form ensures that its fruits are very exposed to the wind, a high percentage of fruits are found on plants as late as the middle of May (Lhotska, 1973).

Wind. The presence of the plume on the achene makes C. vitalba particularly well adapted to dispersal by wind. The growth habit of the plant also gives maximum exposure of the seeds to the wind and maximum distance off the ground achieving greater dispersal distances. The dispersal unit is usually the achene and the plumose style (Fig 3.1), but clusters of seed are often found on the ground with the hairy styles intertwined.

Sitte (1974) examined the importance of the hairy style for dispersal of Clematis species. It was found that in moist conditions the hairs remained parallel to the styles pointing towards the stigma. As the air dried the style hairs spread and pointed towards the base at an angle of 120^{o} (Fig 3.2). This spreading had a considerable effect in reducing the falling speed of the fruit but is surpassed by the mechanisms of other fruits. Exposure to wind is extremely important for dispersal. Clematis has no abscission zone between the fruit and the receptacle but has to be torn off by wind. As a result seeds are only released under conditions promoting distribution despite the inefficient "parachute" apparatus. Removal from the mother plant requires leverage which depends on the feathery style.

When the achene reaches the ground, variations in humidity result in bending movements of the plume. These movements of the plume move the seed backwards and forwards on the ground until the seed becomes lodged in a crack in the soil. Further movement will push the seed into the ground (Paturi, 1976).

Animals and Birds. The plumose style makes the seed of C. vitalba attractive to birds as a nest building material (Atkinson, 1982). Animal dispersal is also possible as the hairs on the plume catch and stick to fur and hair. Human activities also provide a means of dispersal, in particular in soil on machinery, stock and in hay. C. vitalba is sold as an ornamental in some areas and provides a seed source.

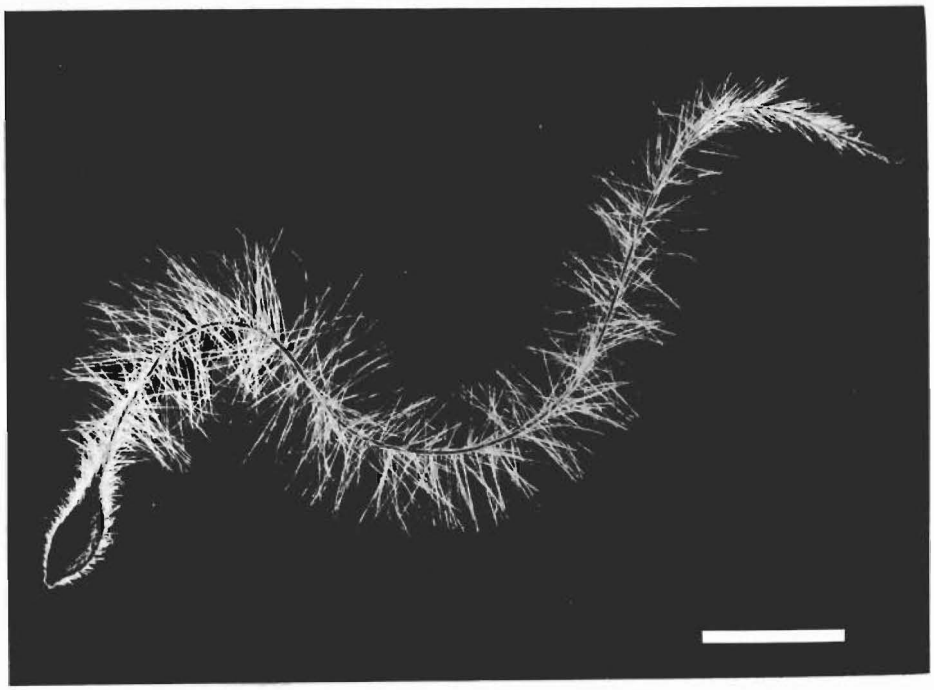


Fig 3.1 Achene of C. vitalba with plumose style (bar=5 mm).

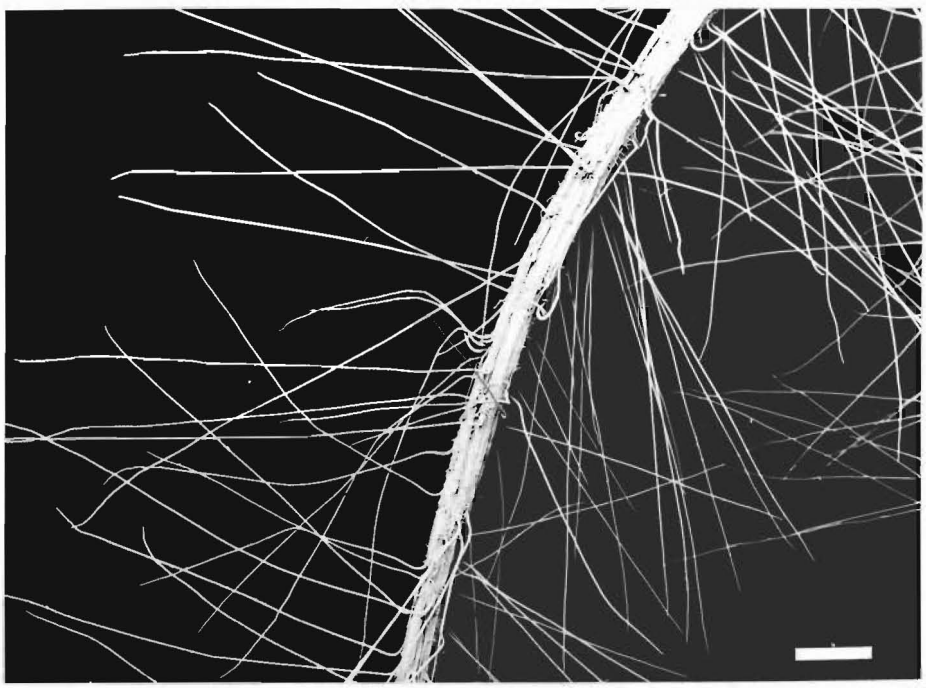


Fig 3.2 Scanning electron micrograph showing style hairs in the dry position (bar=400 µm).

3.2 MATERIALS AND METHODS

Seed Preparation. Before all germination experiments seeds had their styles removed. This was to allow more seeds to be placed in each petri dish and to make counting easier. To check that this procedure was not affecting germination, the germination of treated and untreated seeds was compared. It was found that the removal of styles did not affect germination.

Growth Room Conditions. The growth room used in the germination tests was set at 22 C light and 13 C dark with a 16 hr photoperiod. Preliminary experiments showed these to be the most effective conditions available for germination.

3.2.1. Reproduction

Vegetative Reproduction. Sections of young, woody stem containing two nodes were cut from a mature vine in April. Cuttings were placed in a 1:1 mix of sand and loam with the lower node covered and placed in a glasshouse with automatic overhead watering.

Seed Production. An estimation of the seed production of mature vines of C. vitalba was made over the 1984 season at Carlton Mill Road-Bealy Avenue corner. A sample of 20 seed heads were collected in June 1984 and the number of seeds per head counted. Tests of germinability and viability were made on seeds from 10 samples of seed heads. The number of heads per panicle and the number of panicles/0.5 m^2 were counted in 10 randomly selected 0.5 m^2 quadrats. From this information the mean number of seeds produced in 0.5 m^2 and the estimate of percentage viability was calculated.

The germination tests were carried out in a growth room for six weeks. Viability tests were made using a method described by Moore (1973) in which a 1% solution of tetrazolium (2,3,5,triphenyl-tetrazolium chloride) is applied to the seeds to be tested. Incubation of seeds split through the embryo in tetrazolium results in viable embryos staining bright pink. Seeds in tetrazolium are kept

in the dark at room temperature for 24hr during incubation.

3.2.2. Viability After Burial

Seeds collected in August 1984 and stored dry in a paper bag were buried in early December and late January 1985. Before burial seeds were placed in nylon mesh to aid retrieval. Seeds were buried to a depth of not less than 10cm below the surface in the Botany department shade house, University of Canterbury. The soil in the shade house is kept moist with frequent watering. Seeds were dug up in early June 1985, seven and five months after burial. Samples of each of 7 and 5 month seeds were tested for germination in a growth room for six weeks.

3.2.3 Chilling Requirement

Experiment 1. Seeds were collected from mature vines on Carlton Mill corner, Christchurch in May, June, August and September to determine how early in winter the chilling requirement was met. Further collection of seed was not made as by October seed not dispersed was covered by new seasons foliage. Seeds were stored dry until testing. In November a germination test was carried out in the growth rooms. The total % germination was compared using a Student t-test.

Experiment 2. The effect of the amount of pre-chilling given to seeds on germination was examined. Seeds were collected in May before significant frosts had occurred The seeds with styles removed were then chilled moist at 5 C for 0, 2, 4, 6, and 8 weeks on glass fibre filter paper. After chilling for the required time they were transferred to a growth room. Four replicates of treatments were placed in a randomised block design on the growth room bench. Seeds were checked daily for evidence of germination. Germination was taken as the first appearance of the radicle.

Analysis. The rate of germination was analysed using Probit analysis from the Maximum Likelihood Program (MLP).

3.2.3. The Effect of Light On Germination

Shade. Seeds of C. vitalba with styles removed were

pre-treated with GA_3 to break dormancy. Seeds were sown in 7cm Winstone propagating tubes in potting mix at a rate of 30/pot and arranged in a random block design on the glasshouse bench. Four levels of shading were produced using shade cloth in one, two, and three layers. Individual covers were made for propagating tubes by cutting 17 x 63 cm pieces of shade cloth. The pieces of shade cloth were then folded in half and stapled. The resulting covers were 31.5 cm in height. Shade levels produced were given as a percentage of full light as measured with a Li-Cor photometer with PPFD sensor. Photometer measurements were made in a Temperzone Controlled Environment Chamber under constant light conditions (Table 3.1).There were 4 replicates of each treatment. A count of seeds germinated was made daily to determine the rate of germination. Seedlings were removed as they appeared.

Analysis. The rate of germination was analysed using Probit analysis from MLP.

Light Quantity. Seeds of C. vitalba with styles removed were placed in petri dishes on glass fibre filter paper and moistened. Those treatments to be placed in the dark were moistened in the dark and wrapped in foil. All treatments were then placed in the cool room at 5 C for four weeks. After that time the treatments were placed in a growth room. The dark treatment had eight replicates and the light had four replicates. Half of the dark replicates were opened daily along with the light treatment and the number of germinated seeds counted for six weeks. The other four dark replicates remained unopened throughout the course of the experiment. At the end of the experiment the ungerminated total dark treatments were left in the light and further germination recorded for the next two weeks.

Analysis. Total % germination between the treatments was compared using one way Analysis of Variance. No comparison was made using the seeds germinated after transfer to light.

Shade Cloth Layers	% Full Light
0	100 ± 0 (S.E)
1	45 ± 0.4
2	22 ± 0.7
3	14 ± 0.3

Table 3.1 Levels of shading produced using shade cloth.

3.3 RESULTS

3.3.1 Reproduction

Vegetative Reproduction. After eight months cuttings had failed to produce either roots or new shoots. No living tissue appeared to be present.

Seed Production. The estimation of the number of viable seeds per 0.5 m^2 which C. vitalba can produce is given in Table 3.2. It should be noted that the site, Carlton Mill corner, is near the central city and along a busy arterial route. Growth and seed production may be limited by city pollutants.

Seed Dispersal. Although the dispersal unit is the achene and style, seeds are often found on the ground clumped together with the hairy styles intertwined. These clumps of seeds also appear to be dispersed by wind rolling them along the ground. Seeds of C. vitalba also appear to be suited to water dispersal. Seeds were found to be light and floated well on water. Since this species is often observed growing along water courses in Christchurch, water is possibly an important means of dispersal. The plumose style aids floatation on the water by increasing surface area.

3.3.2. Viability After Burial

C. vitalba seed lost viability during burial in the soil (Table 3.3). Examination of seeds after burial revealed that all but the pericarp tissue had decomposed. Seeds collected in late July 1982 and stored dry in a paper bag still had high germination rates when tested in March 1984.

	Mean	S.E.	Range
No. Seeds/ Receptacle	21.9	± 1.0 (n=20)	12-28
No. Heads/ Panicle	21.2	± 2.3 (n=20)	5-39
Panicles/ 0.5 m^2	38.0	± 5.1 (n=10)	10-63
% Viability	73.4	± 5.5 (n=10)	33-90
Estimate No. Seeds/ 0.5 m^2	17650		

Table 3.2 Seed Production by C. vitalba

	Length of Burial	
%	4 months	7 months
Viable	1.3	0

Table 3.3 The Effect of Burial on C. vitalba Seed Viability.

3.3.3. Chilling Requirement

Seed Maturation Over-winter. Seed maturation over winter (Table 3.4) was found to be a slow process. Seeds were found to remain in an immature state until August. By September a significant increase in total percent germination had occurred. Seed not dispersed by October was trapped in new seasons foliage.

Pre-chilling. The zero weeks treatment was excluded from the probit analysis as only one seed germinated. The eight week treatment was also excluded from analysis as fungal infection of seeds affected the germination response. In earlier experiments seeds were treated with a 1.5% solution of 1% hyperchlorite solution to prevent fungal infection. The hyperchlorite was found to significantly affect germination so was not used in this experiment.

Chilling was found to significantly reduce the time to 50% germination (Table 3.5). Increasing the period of chilling increased the germination rate (Fig 3.3). The slope of the lines produced by the probit analysis suggest that other factors interacted with the germination response. A chi-square test between lines found them to be significantly different. Although the rate of germination increases with chilling, the time between radicle emergence and 50% germination also increases with chilling.

Gibberellin Inhibition. The time to 50% germination was not significantly affected by treatment with CCC (Table 3.6). There was no significant difference between the response lines produced by the probit analysis (Fig 3.4).

3.3.3. Light

Shade. The time to 50% germination was significantly reduced by shading (Table 3.7). There was no significant difference between shaded treatments. The slopes of the lines produced by the probit analysis (Fig 3.5) were not significantly different.

Light Quantity. Total darkness significantly reduced total percent germination (Fig 3.6). Short exposure to light was found to significantly increase total percent germination in comparison to longer exposure

(16 hr photoperiod) to light. When seeds from the total darkness treatment were transferred to the long day (LD) treatment 45.5% (± 2.1) germinated.

Month	Total % Germination
May	0 a
Jun	0 a
Aug	4.17 a
Sep	22.51 b
S.E.(n=4)	1.32
C.V.%	39.59%

Table 3.4 Over-winter Maturation of C. vitalba Seed.

Means followed by the same letter are not significantly different (P>0.05) as determined by Duncan's Multiple Range test.

Chilling (Weeks)	Days to 50% Germination	Confidence Limits		Intercept	Slope
2	13.00	12.74	13.33	-0.43 ± 0.06	13.45 ± 1.1
4	10.20	9.94	10.00	0.02 ± 0.04	7.3 ± 0.4
6	6.18	5.92	6.42	0.54 ± 0.04	4.94 ± 0.23

Table 3.5 The Effect of Chilling on the Time to 50% Germination in C. vitalba.

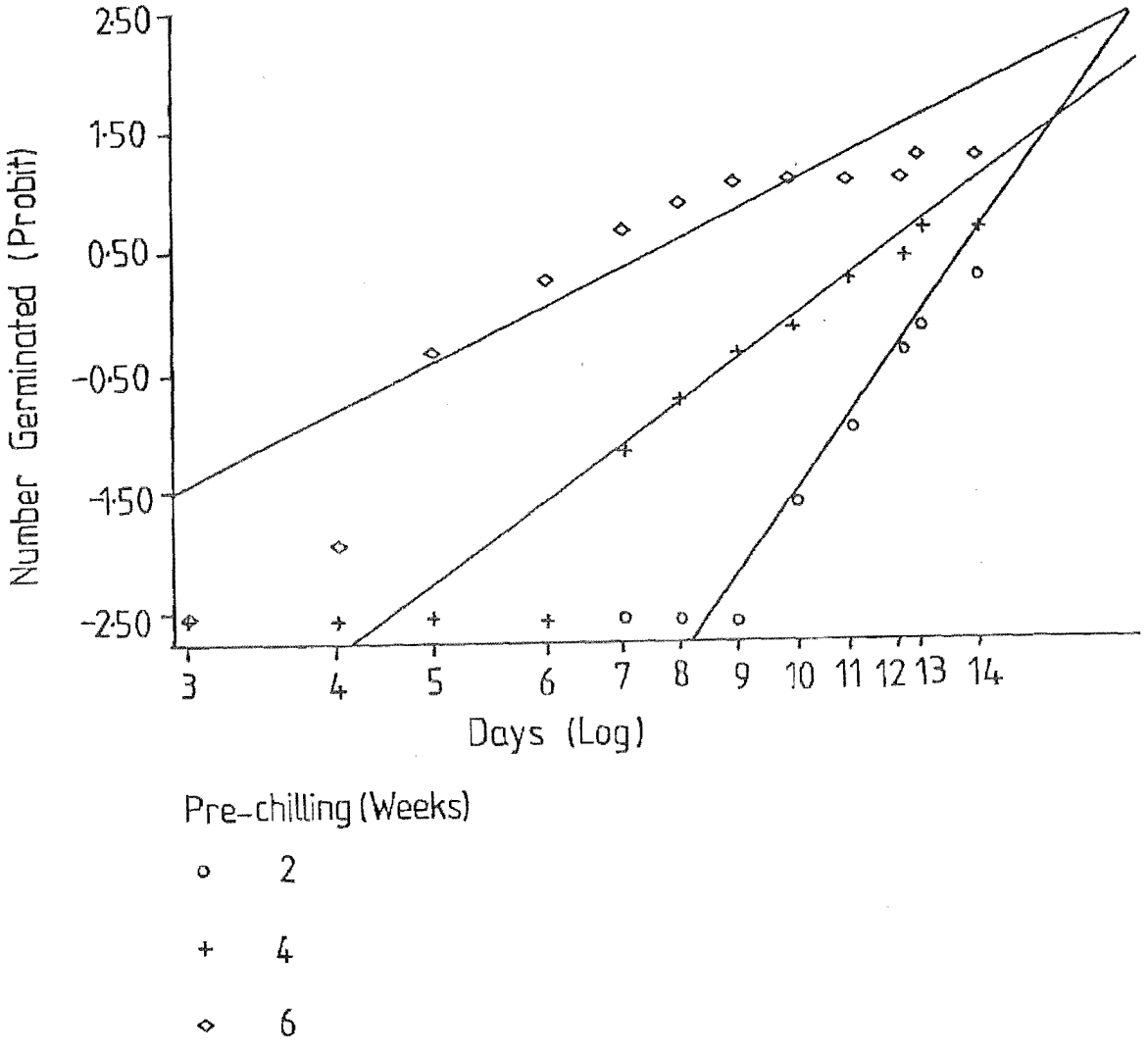


Fig 3.3 The effect of pre-chilling treatment on the rate of germination in C. vitalba.

CCC	Days to 50% Germination	Confidence Limits	Intercept	Slope
0	8.74	8.40 9.12	-0.15 (±0.1)	5.44 (±0.4)
+	8.9	8.68 9.19	-0.12 (±0.1)	8.5 (±0.6)

Table 3.6 The Effect of 2-chloroethyltrimethylammonium chloride (CCC) on the Time to 50% Germination in C. vitalba.

% Total PPFD	Days to 50% Germination	Confidence Limits	Intercept	Slope
100%	24.77	24.43 25.17	-0.34 ±0.05	18.07 ± 0.6
45%	23.24	22.99 23.51	-0.05 ± 0.05	18.63 ± 1.1
22%	23.18	22.88 23.50	-0.06 ± 0.04	15.41 ± 1.0
14%	22.68	22.44 22.95	0.08 ± 0.05	17.79 ± 1.0

Table 3.7 The Effect of Shading on Time to 50% Germination in C. vitalba.

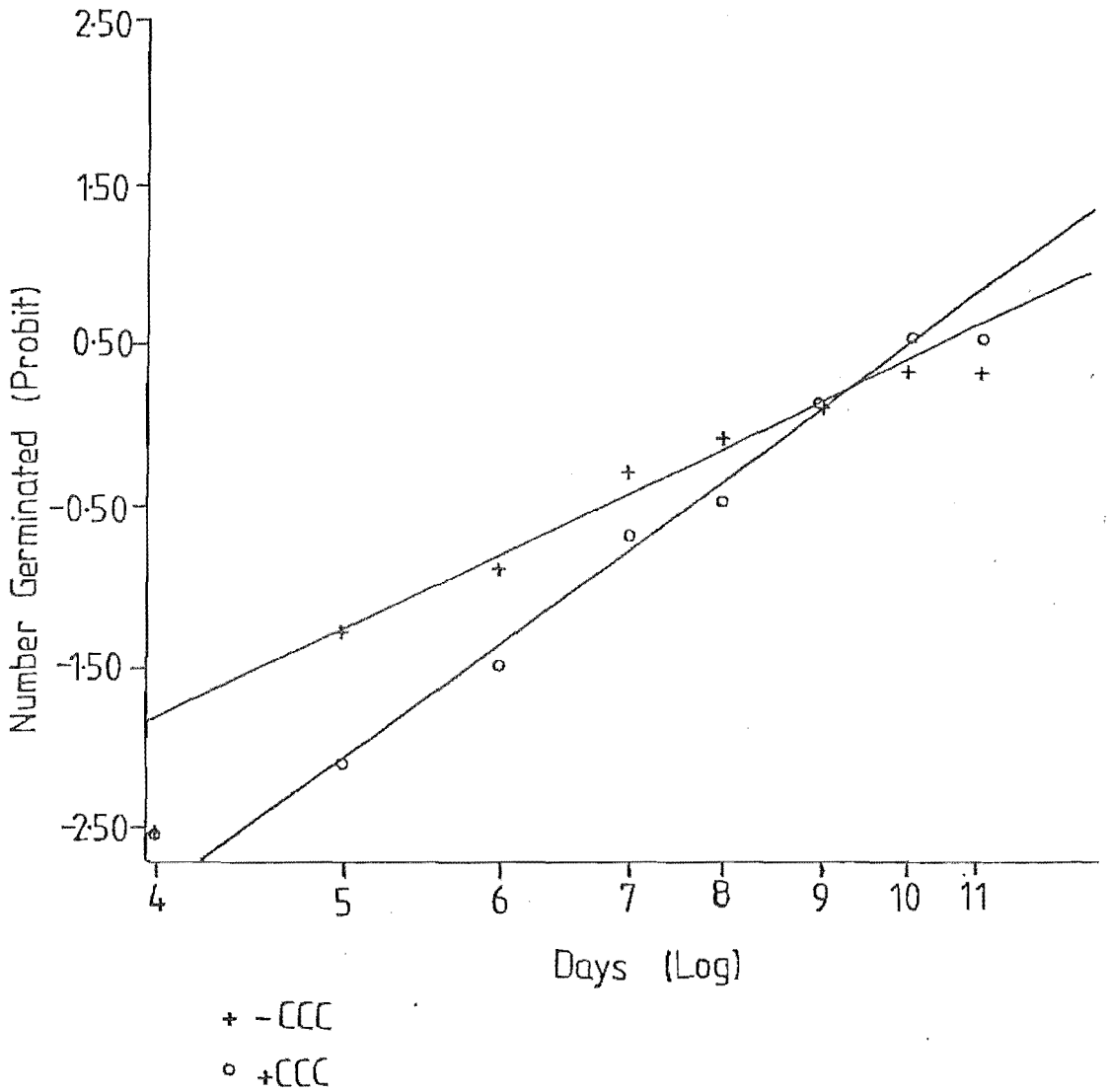


Fig 3.4 Effect of CCC on the rate of germination in C. vitalba.

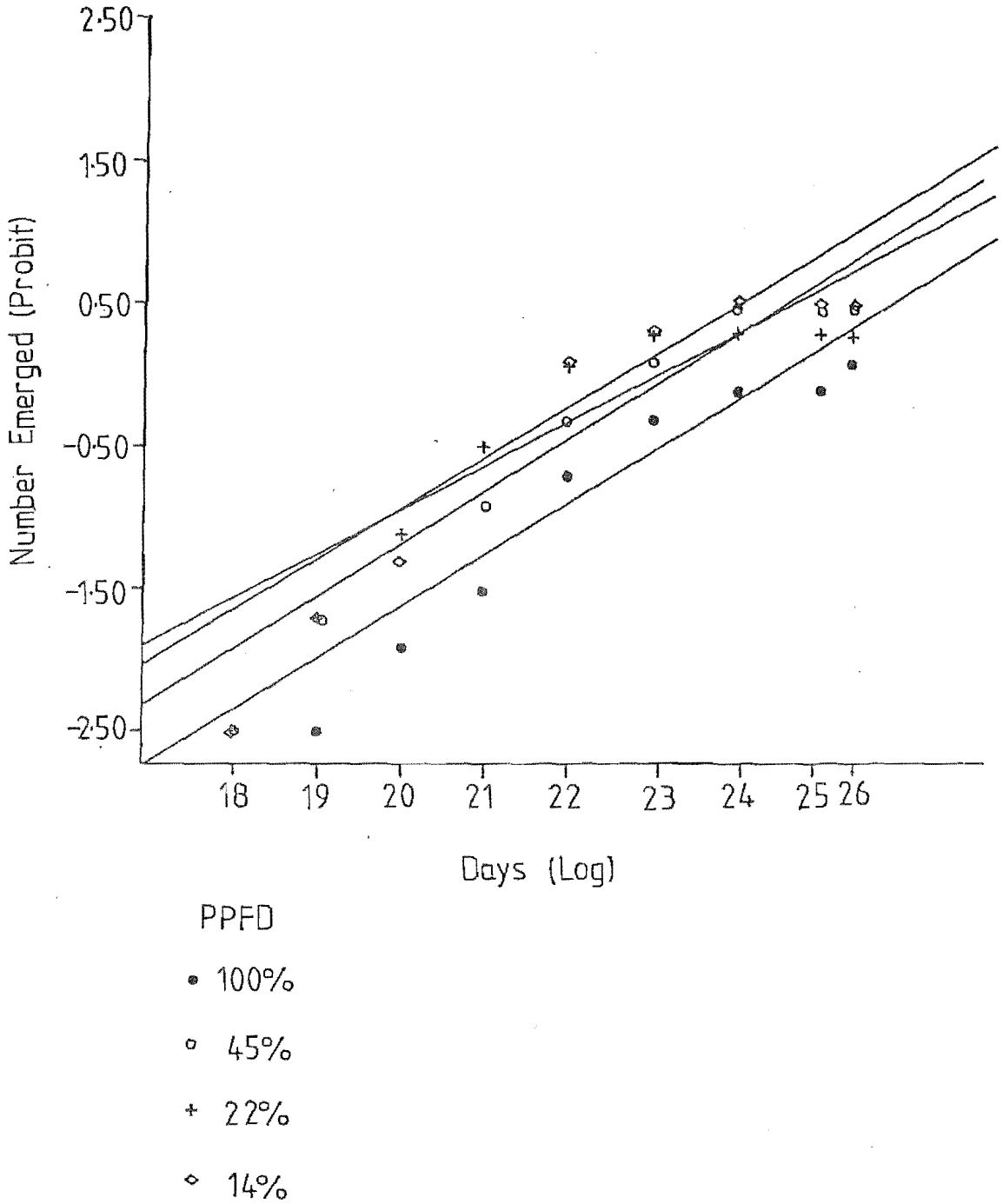


Fig 3.5 The effect of shading on the rate of germination in C. vitalba.

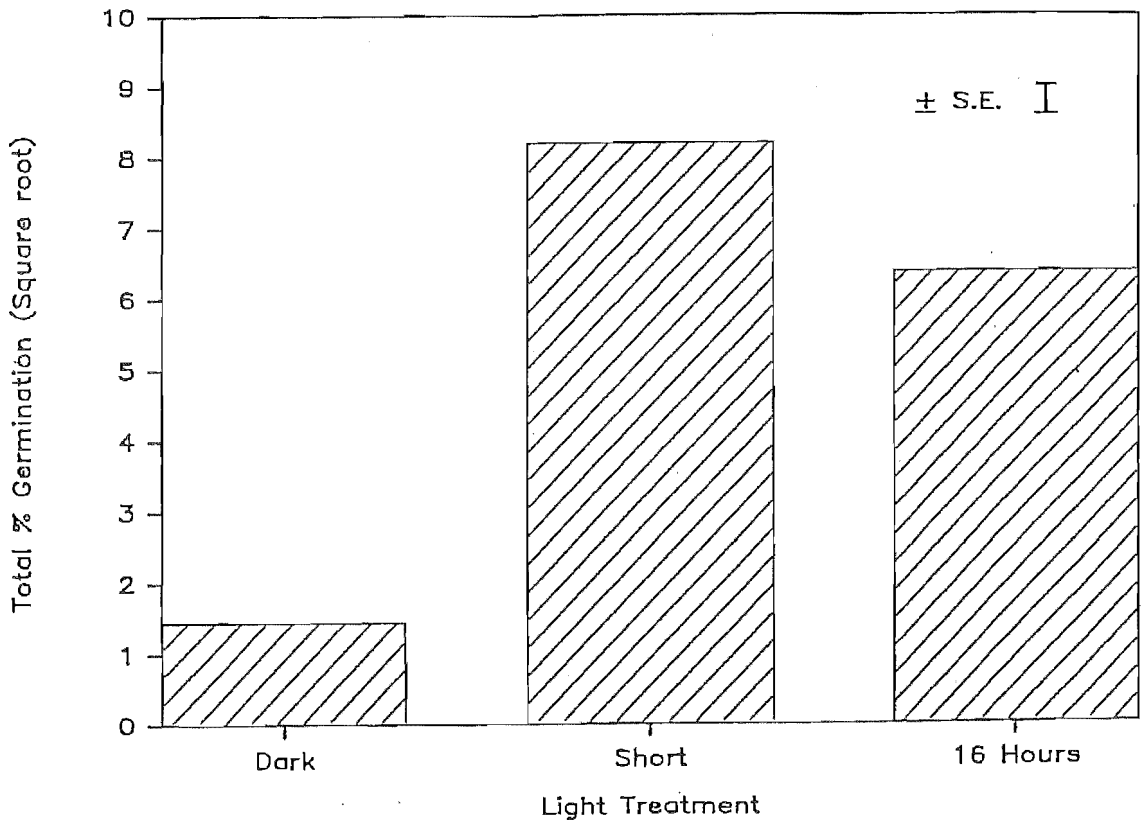


Fig 3.6 The effect of light quantity on total percentage germination in C. vitalba.

Fig 3.7 C. vitalba growing on vegetation along the road margin of the Puhi Puhi Scenic Reserve.

3.4. DISCUSSION

3.4.1. Reproductive Capacity

Characteristics of a successful weed species includes a high reproductive capacity. In a perennial species part of its reproductive capacity may be an ability to reproduce vegetatively (Hill, 1980). C. vitalba reproduces vegetatively when stems produce roots at the nodes (Fig 1.3). In most cases these stems remain part of the plant. However, should part of the plant die or be destroyed, the rest will continue to grow.

The ability to root at the node does not appear to be an important factor in dispersal. Fragments of young stem from mature plants failed to produce roots after eight months. Stems of the same age on young plants produced roots at the node on the glasshouse bench after three months. When still attached to the parent plant the ability to root at the node is possibly more important for water and nutrient supply to a large vine than for dispersal in space. However rooting at the node is possibly quite important for dispersal in time, as it would keep the plant alive at the site for longer if the original stem was damaged.

Mature vines of C. vitalba have a high reproductive capacity (Table 3.2). Areas of plant each 0.5 m^2 produced an average 13000 viable seeds per year. When established, plants of C. vitalba can cover large areas of ground or forest canopy (Fig 3.7). Although seed production is high the viability of seeds is quickly lost if the seeds are buried (Table 3.3). It is possible that viability is retained longer in the field than suggested by the results of this study. The soil in which the seeds were buried was maintained in a moist state. In drier soils C. vitalba seeds may possibly maintain their viability longer. Further experimentation is needed to determine the effect of substrate moisture content on seed viability. If it is found that seeds do not retain their viability it would mean there was no seed bank of C. vitalba in the soil. As a result once adult plants were controlled in an area checks for regeneration would be unnecessary after the first year.

3.4.2. After-ripening

Seeds do not reach maturity under natural conditions until early spring. This coincides with the time of dispersal (Chapter 2) and possibly the most favourable conditions for germination and seedling establishment. C. vitalba has an immature embryo (Lhotska, 1974) and requires a period of after-ripening before germination will occur. An after-ripening requirement can often be overcome by a period of chilling (Kramer and Kozlowski, 1979).

Seeds collected in May were found to have the time to 50% germination significantly reduced by increasing periods of chilling at 5 C. Seeds which were not chilled before germination tests did not germinate. Seeds in natural conditions on the vine are subjected to short periods of chilling throughout winter. The period of chilling which resulted in the shortest time to 50% germination was six weeks. The eight week treatment was destroyed by fungal infection. It is possible that the other treatments were also affected by fungal infection or anaerobic conditions which reduced viability. This is demonstrated by the significant difference between the response slopes (Fig 3.3).

C. vitalba has a chilling requirement for seed germination. This is satisfied by exposure to winter temperatures in a temperate climate. The change of seed colouration (Chapter 2) with the first frosts possibly signifies the beginning of seed maturation. This would limit the distribution of C. vitalba to areas which have winter temperatures low enough to fulfill this requirement. This may explain its absence north of Auckland and tendency not to spread in other northern areas.

Treatment with the gibberellin inhibitor CCC (Fig 3.4) did not affect the time to 50% germination or total percent germination. It is likely that gibberellins are not involved in the dormancy breaking mechanism in seeds of Clematis. Another possibility is that the concentration of inhibitor used was not strong enough to inhibit gibberellin synthesis. It was thought that spraying CCC on seeds while still present on the vine might slow germination long enough when they were dispersed to reduce viability. The results indicate that spraying of 10^{-3} M CCC would not be

effective.

3.4.3. Light

Germination of C. vitalba appears to be inhibited by high PPFD. In the shading experiment seeds in the 100% total PPFD treatment took significantly longer to reach 50% germination (Table 3.7). Total percent germination did not differ between treatments. This may represent a strategy to ensure rapid germination and seedling establishment when shaded. In deciduous forests in early spring this may allow C. vitalba to germinate and establish before bud burst and leaf expansion of the tree canopy is completed.

Light quantity affects total percent germination. A significantly higher percentage of seeds germinated in response to short exposure to light than to L.D. light conditions. The response of C. vitalba seeds to total darkness differed from the response described by McClelland (1979) and Tucker (1978). Both found that high percentages of germination occurred in total darkness treatments wrapped in foil. In this study it was found that germination in total darkness was almost nil. In the short exposure treatment where petri dishes were wrapped in foil except when germinated seeds were counted, percentage germination was high. The results of McClelland and Tucker suggest that they may have opened foil covered treatments in the light.

When the dark treated seeds were transferred to LD light conditions the percentage that germinated was similar to the LD treatment. This demonstrates a light requirement for germination in C. vitalba.

There was an inhibition of germination found in the LD treatment compared to the short exposure treatment. This suggests possible adaptions to germination during SD conditions. However, Tucker (1978) found that treatment of C. vitalba seeds with SD and LD exposure did not produce a significantly different response. It has been suggested that the observed differences in responses may be due to the presence of different ecotypes (Atkinson, 1982).

High total percentage germination occurred after short exposure (5 minute)to light. Short light breaks may simulate sunflecks, which would signal the presence of a canopy gap

to the seed, allowing seeds to germinate after a canopy disturbance. Observations of the life history of C. vitalba indicate that in the natural situation germination occurs in early spring (Chapter 2). Inhibition by LD conditions would reduce germination in summer when conditions might be more likely to be unfavourable for establishment. Further study is necessary to resolve the effect of different lengths of light exposure on germination of C. vitalba.

CHAPTER 4

SEEDLING ESTABLISHMENT

4.1 INTRODUCTION

The distribution of C. vitalba in Europe and New Zealand gives some indication of its requirements for growth. Seedling establishment is a critical phase in the development of a plant. Factors that may be important in establishment were studied. The literature suggested that the factors most affecting the distribution of C. vitalba include light, soil fertility (Ellenberg, 1974; Atkinson, 1982), soil pH (particularly base status) (Ellenberg, 1974; Salisbury, 1952; Mitchell, 1975) and soil physical factors (Sankey, 1966; Ellenberg, 1974). In New Zealand high densities of C. vitalba are associated with particular forest types, particularly broadleaf or podocarp forests (A.T. Dobson, pers. comm). This suggests that these forest types may be more susceptible to invasion by C. vitalba.

Ellenberg (1974) described C. vitalba as a "half light plant" with a preference for sites where it receives at least 50 percent of full light. In New Zealand forests it has been observed that seedlings establish mainly along forest margins or in canopy gaps (Atkinson, 1982).

Tucker (1978) conducted experiments in both field and glasshouse conditions. It was found that shaded plants in the glasshouse had larger leaves, while plants from the light were heavier and had double the root biomass. The plants in the shaded treatment received 21% of the photosynthetically active photon flux density (PPFD) received by plants in the light treatment. In the field over a period of three months all tagged seedlings in the shade died while 40% of those in the light survived. Tucker (1978) concluded that it was not possible to deduce specific light requirements from these experiments.

The distribution of C. vitalba in the British Isles has been correlated with the occurrence of limestone outcrops (Perring and Walters, 1962). Salisbury (1921) noted that many obligate calcicoles of moist climates are much less edaphically restricted in arid conditions. Within limited geographical areas there is a strong relationship between calcicoles and substratum. Interpretation becomes complicated by the wider distribution of such plants in drier parts of Europe (Etherington, 1982).

The association of C. vitalba with calcareous soils in the British Isles led to its classification as a calcicole (Salisbury, 1952; Sankey, 1966). However in Europe, particularly in more southern regions, C. vitalba tolerates a wider range of soils. The physical conditions of the soil seem to have a greater influence on growth (Sankey, 1966). The occurrence of C. vitalba on shallow soils over chalk and limestone (Sowerby and Sowerby, 1899) does not necessarily suggest its calcium requirement is high. Soils over chalk and limestone tend to be well-drained (White, 1979; Sankey, 1966). C. vitalba is found in warm oceanic climates, on well-drained soils in Europe (Ellenberg, 1974).

Tucker (1978) compared the growth of C. vitalba seedlings in soil treatments lacking essential nutrients to a control containing all essential elements. He found that seedlings grew better in soil lacking iron. Biomass was reduced in comparison to the control in the treatments which lacked nitrogen, phosphorus or sulphur. Plants grown in the minus phosphorus treatment had purple pigmented leaves. The absence of calcium resulted in the death of all seedlings in that treatment.

A preliminary experiment found differences in response to soils from different vegetation types. Plants grown in soils with a lower pH had stunted growth, red-purple leaves and stems. Phosphorus deficient plants tend to develop red pigmented leaves and have stunted growth (Salisbury and Ross, 1979). This experiment suggested that phosphorus deficiency might be an important factor in preventing C. vitalba establishing in these soils. However calcium deficiency or iron or aluminium toxicity may be implicated. In the field the effect of vegetation type and

environmental factors on seedling establishment were examined. In addition, the effect of light, soil moisture, and soil type with phosphorus and calcium addition were studied under controlled conditions in the glasshouse.

4.2 MATERIALS AND METHODS

4.2.1 Transplant Experiment

Seedlings. C. vitalba seeds were treated with GA_3 10^{-4} M before being sown in seed trays. Germination occurred after three weeks. In late October two week old seedlings were transplanted into 15 selected sites in Kaikoura Reserves (Fig 4.1). Seven seedlings were transplanted at each site.

Sites. The sites were chosen for their different vegetation types and ground cover. The vegetation types were broadleaf, kanuka, broadleaf-podocarp, beech forest and a disturbed site. The disturbed site consisted mainly of tree fern, grasses and young broadleaf and podocarp seedlings.

Within each vegetation type microsites were selected consisting of open ground, grass canopy, fern canopy and tree fern canopy where these were present.

Puhi Puhi Scenic Reserve (Fig 4.2). This reserve is situated 15km from Kaikoura on the West bank of the Puhi Puhi River, just below its junction with the Clinton River. It covers an area of 14.8 ha on a small river terrace. The margins are severely infested with C. vitalba which appears to be spreading (Williams, 1982) (Grid Ref.: NZMS 1 S49 018073).

Blue Duck Scientific Reserve (Fig 4.3). This reserve is situated 18km from Kaikoura on the Western side of Iron Gate Valley on the Seaward Valley Road. It covers an area of 85.4 ha on hillslopes, spurs and minor valleys. The reserve is surrounded by farmland and scrub (Williams, 1982). C. vitalba is not present in this reserve (Grid Ref.: NZMS 1 S42 & S43 067112).

Kowhai Bush (Fig 4.4). (Marlborough Catchment Board River Protection Reserve) Kowhai Bush is situated 8 km North-west of Kaikoura on the North bank of the Kowhai River

(Hunt and Gill, 1979). It covers an area of approximately 355 ha (Hunt, 1979) on river flats surrounded by farmland. There are serious infestations of C. vitalba in this reserve particularly at the more disturbed eastern end (Fig 4.5) (Grid Ref.: NZMS 1 S49 902945).

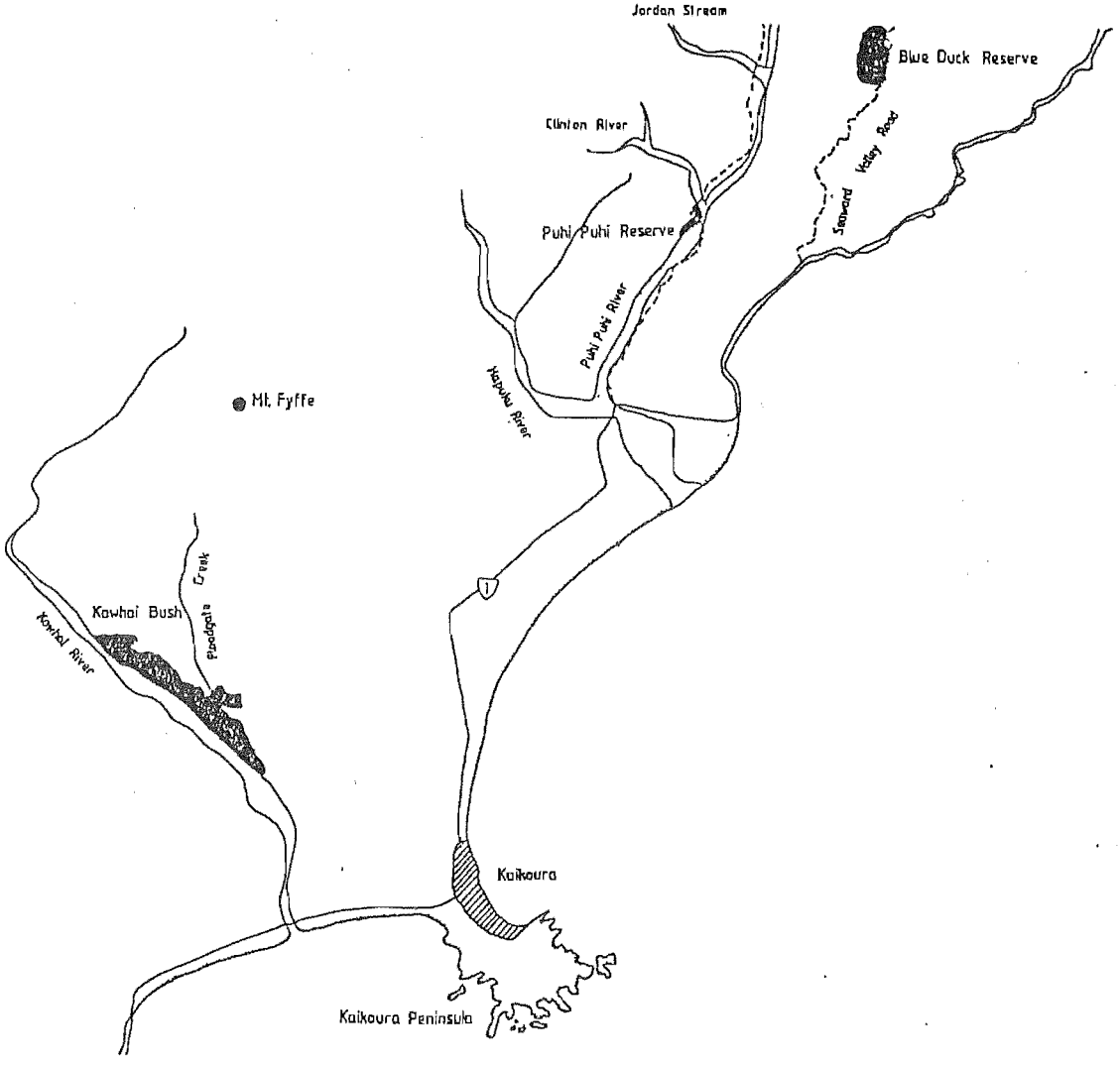


Fig 4.1 Map showing location of Reserves used in this study.

	Puhi Puhi	Blue Duck	Kowhai Bush
Soil Physical Aspects	Hygrous rendzina (Kaitoa) and Recent alluvium	Lowland yellow-brown earth (Patutu)	Wairau Sandy loam with Boulders
Soil Parent Material	Alluvium	Slope detritus	Alluvial gravel
Geology	Argillaceous Limestone (Amuri) & redeposited material	Upper Cretaceous sedimentary deposit	Greywacke with other types present e.g. Limestone
Altitude (m)	150-200	300-457	50
Aspect	Flat	Mostly E & NE. Some SE	Flat
Rainfall	1200mm	1100mm	1441mm
Natural Fertility	Medium-High	Moderate	Medium-High
Drainage	Good	Good	Rapid

Table 4.1 Physical Characteristics of Kaikoura sites. (Gibbs and Beggs, 1953; Williams, 1980; Hunt and Gill, 1979)

Fig 4.2 Puhi Puhi Scenic Reserve, Puhi Puhi Valley, Kaikoura.

Fig 4.3 Blue Duck Scientific Reserve, Iron Gate Valley, Kaikoura.

Fig 4.4 Kowhai Bush, Marlborough Catchment Board River Protection Reserve, Kaikoura.

Fig 4.5 Aerial view of the eastern end of Kowhai Bush with C. vitalba in the canopy (arrowed).

List of Seedling Transplant Sites

Puhi Puhi Reserve (Broadleaf-Podocarp)

1. Open Canopy
2. Closed Canopy

Blue Duck Reserve (Podocarp)

3. Open Canopy
4. Grass Canopy

Blue Duck Reserve (Beech)

5. Open Canopy
6. Closed Canopy
7. Grass Canopy

Blue Duck Reserve (Regeneration)

8. Open Canopy
9. Grass Canopy
10. Tree fern Canopy

Kowhai Bush (Broadleaf)

11. Open Canopy
12. Grass Canopy
13. Fern Canopy

Kowhai Bush (Kanuka)

14. Open Canopy
15. Fern Canopy

Description of Site Vegetation

Puhi Puhi Scenic Reserve

Vegetation under both the open and the closed canopy was similar. The main difference was in light attenuation. The sites were located in the area mapped by Williams (1982) as Habitat 2. The ground layer of these sites was sparse and the shrub layer mainly consisted of Macropiper excelsum (kawakawa). The canopy consisted of P. spicatus (matai) and Podocarpus totara (totara). Broadleaf species included Hedycarya arborea (pigeonwood) and Alectryon excelsus (titoki). Climbers present were Metrosideros diffusa (rata), Ripogonum scandens (supplejack) and a Parsonsia species. C. vitalba is also present on the margins of the reserve but not at this site.

Blue Duck Scientific Reserve

Podocarp Site. The canopy was similar between the two sites in this vegetation type. It consists of mixed podocarps including totara, Podocarpus hallii (halls' totara), matai and P. ferrugineus (miro) with P. dacrydiodes (kahikatea) nearby. The shrub layer in the open site is sparse. It consisted mainly of Macropiper excelsum and Elaeocarpus hookerianus. The ground layer had a thick leaf litter and very few plants.

The grass canopy site consisted of a ground layer of Uncinia species with Blechnum discolor and some Asplenium species present. The shrub layer consisted of Coprosma species, Carpodetus serratus (marbleleaf) seedlings, Macropiper excelsum, and Cyathea dealbata. Climbers present at both sites included Metrosideros diffusa and M. perforata.

Beech. The canopy vegetation of these sites consisted of a pure stand of Nothofagus solandri var. solandri (black beech). The sites consisted of an open canopy, grass canopy and tree fern canopy. The main differences between the beech sites was the presence of Microlaena avenacea species in the grass site and Cyathea dealbata in the tree fern site. The open canopy site had a ground layer consisting of a thin leaf litter. The shrub layer consisted of seedlings of halls' totara, pigeonwood, Pseudopanax arboreus, Pittosporum eugenioides (lemonwood),

Coprosma species and Pennantia corymbosa. Cyathea dealbata was also present. The ground layer was mainly of bare ground covered with a thin leaf litter. In areas where canopy gaps occur there were large patches of Microlaena species, marbleleaf was also present in the canopy gaps.

Disturbed. The sides of the gullies are very steep in this reserve. This has resulted in a large number of slips which have altered the structure of the vegetation. The gully sides had a distinct vegetation consisting of many broadleaf tree and seedlings, including Melicytus ramiflorus (mahoe), Pseudopanax arboreus, Elaeocarpus dentatus and Coprosma australis. Podocarp seedlings were also common. Large areas were covered with Cyathea dealbata. The open canopy site was characterised by mainly bare ground and some adventive herbs and grasses including Holcus lanatus and Hypochoeris radicata. The grass canopy consisted of Uncinia species; seedlings of Cyathodes fasiculata were also present. The tree fern canopy consisted of Cyathea dealbata. The understorey of the tree fern was mainly tree fern litter but some plants of Cyathodes fasiculata, Blechnum discolor and Metrosideros diffusa were present.

Kowhai Bush River Protection Reserve

Broadleaf. This site is in the area described by Dobson (1979) as Habitat 4. The canopy consisted of mixed broadleaf tree species, the dominant species being mahoe. Other species present included marbleleaf, Pittosporum tenuifolium, Griselinia littoralis, Pseudopanax arboreus and Sophora microphllya. The shrub layer included Coprosma robusta, Olearia paniculata, Dodonaea viscosa, Astelia fragrans and Cordyline australis. Also present were several mature trees of Leptospermum ericoides (kanuka). The ground layer consisted of Uncinia species and Phymatodes diversifolium and some small areas of bare ground.

Kanuka. This site is in the area described as Habitat 3 (Dobson, 1979). The canopy consisted of mainly kanuka, some Leptospermum scoparium (manuka), mahoe, Griselinia littoralis and Pittosporum tenuifolium trees were also present. The understorey consisted of Olearia paniculata, Coprosma australis, Pseudopanax arboreus and Corokia cotoneaster. The ground layer was mostly comprised of Phymatodes diversifolium, some areas of bare ground, and a few clumps of Uncinia species.

Physical Factors

Temperature. Temperature was measured using maximum-minimum thermometers which were placed out on three occasions during the growing season for periods of six days at a time. The temperatures obtained at each site were compared to temperatures recorded at Kaikoura over the same period. This enabled the difference between the temperature data from the meteorological station in Kaikoura and the Reserves to be estimated.

Irradiance. Intergrated light measurements were obtained for each site using Ammonium diazo paper light sensors based on a technique described by Friend (1961). Each light sensor consisted of a stack of 15 sheets of diazo paper cut into 30mm x 30mm squares and stapled to form booklets. The diazo paper was stacked with the light sensitive side up with a sheet of black paper top and bottom (Young and Whitehead, 1981).

To keep sensors dry during exposure in field conditions, they were mounted inside plastic petri dishes. The petri dish lid was fitted with a circular piece of black paper with a 20 mm diameter hole cut in the centre. The edges and base were painted black to exclude unwanted light. The booklet was held tightly against the light window with a polystyrene disk. Masking tape was used to hold the lid and base of the petri dishes together and a black removable self-adhesive label used to cover the light window. A velcro strip was attached to the base for attaching to a corresponding velcro strip (Turton, 1982) on stakes left at each site in the field (Fig 4.6). Sensors were transported to sites in a black plastic bag and positioned before

removal of the black adhesive label. Propan-1-ol alcohol was used to clean the light window after removal of the adhesive label. The stakes supporting the sensors were placed approximately 15 cm above ground level. There were three replicates at each site.

After six days exposure, exposure was terminated by the placement of another black adhesive label over the light window. Booklets were developed by suspending above a concentrated ammonia solution in a closed container. In ammonia vapour, unexposed paper changes to dark blue while the light bleached papers remain white.

Ammonium diazo paper is sensitive mainly to the violet and ultraviolet (200-475 nm) end of the spectrum (Federer and Tanner, 1966). The ratio of violet and ultraviolet wavelengths to the photosynthetically active wavelengths was assumed to be constant. Over the same period that light sensors were set out in the field, calibration sensors were set out on an unshaded roof at Kaikoura, next to a LI-COR LI-510 intergrating light meter. Eight sensors were used with two replaced every second day.

The number of calibration sensor papers exposed was regressed against the total irradiance received. The total irradiance was calculated by a LI-COR LI-510 intergrating light meter with PPFD sensor. The regression line produced from the calibration allowed conversion from the number of papers exposed to an estimate of PPFD for each site.

Light intensity is reduced logarithmically as it passes through the layers in the booklet. A method of assessing the partially exposed papers is important. Turton (1982) described a technique of assessing the partially exposed papers using a reflectometer which was used in this study. The number of fully exposed papers was counted. For each booklet the number of fully exposed papers and the fractions given by the reflectometer were summed.

Fig 4.6 Light sensor in Kowhai Bush.

Altitude. The elevation of each site above sea level was determined using a altimeter.

Soil Factors

Soil samples from each site were collected and brought back to the Botany Department for analysis.

Moisture Content. The soil moisture content of soils from each site was determined at three intervals over the summer. Samples were collected from each site and sealed in plastic bags on 13/10/84, 12/12/84 and 20/2/85. In the lab the samples were weighed before drying to constant weight at 105 C. From this information the percentage of moisture present in the soil was determined.

Waterholding Capacity. Samples of soil from each vegetation type were air dried then placed in Gooch crucibles and weighed. The crucibles and soil were then transferred to a tray containing water and left until the soils were saturated. Saturation was taken as the point at which the soil glistened. After saturation was reached, excess water was blotted from crucibles and they were weighed. Crucibles and soil were then oven dried at 105 C for 48 hr. The water holding capacity was calculated and expressed as the percentage of the oven-dry soil (Dewis and Freitus, 1970).

pH. The pH of soils from each site was measured using a pH meter. For each sample 10 cm^3 of air dry soil was mixed with 25 ml of distilled water. The pH measurement was recorded after one hour.

4.2.2. Light

Shade. A glasshouse experiment was designed to simulate different levels of shading. The levels of shading were produced as for the germination experiment in Chapter 3. The shade levels produced are given in Table 3.1.

Pre-germinated seedlings of C. vitalba with one true leaf were transplanted into propagating tubes. The potting mix used was as given in appendix 4. Treatments were arranged in a randomised block design on the glasshouse bench on the glasshouse bench to minimize watering and lighting differences reported by van Gardingen (1983).

Sun and Shade Leaves

Samples were taken of leaves from shaded and full light conditions. Samples were taken from Kowhai Bush from the same locations as those used for gas exchange (Chapter 5).

The internal structure of sun and shade leaves was examined using a Cambridge Instruments Scanning Electron Microscope (Appendix 1). Specimens were prepared using freeze-dry techniques.

4.2.3. Soil Moisture

Pots and Soil. Pots used in the experiment were 460 cm^2 plastic containers. The soil used was collected from Kowhai Bush, a Marlborough Catchment Board Reserve 8 km north-west of Kaikoura.

Soil Drainage. The three levels of soil drainage were simulated by drilling holes at different heights in the plastic containers.

1) Well-drained soil was produced by drilling three 5mm holes at evenly spaced around the base of the pots.
2) Moderately drained soil was produced by drilling two 5mm holes midway up the pot.
3) Waterlogged soil was produced by drilling one 5mm hole in the pot just above soil level.

Pots were filled with 410g of soil and watered until soil was moist.

Seed Treatment. Seeds, with style removed, were pre-soaked in GA_3 10^{-4} M for 3 days. The seeds were planted in a seed box containing potting mix and Osmocote fertiliser (Appendix 4). Germination began after 21 days. Seedlings were transplanted at the one true leaf stage into treated pots on 30th May. The 10 replicates of each treatment were arranged in a completely randomised block design on the glasshouse bench.

Glasshouse Conditions. Were as described in Appendix 3 for over-winter conditions.

4.2.4 Soil Type and Phosphorus and Calcium

A three factor experiment was designed to examine the

effect of addition of phosphorus and calcium on soils from selected vegetation types. The soils were chosen on the basis of a preliminary experiment. The preliminary experiment compared the growth response of C. vitalba in soils from the sites used in the seedling transplant experiment (4.2.1.). This indicated possible nutrient deficiencies in the Blue Duck beech soil. The red-purple colouration of the plants suggested some kind of nutrient deficiency. Tucker (1978) reported that C. vitalba has a high requirement for calcium and phosphorus, so these elements were chosen for the experiment.

The soils used in the three factor experiment were the Blue Duck beech, and podocarp, and the Kowhai Bush broadleaf soil. The podocarp soil was chosen because it occurs in a site adjacent to the beech soil with similar parent material and climate. The Kowhai Bush soil was chosen as a control for the experiment as infestations of C. vitalba occur in Kowhai Bush. There were no infestations of C. vitalba in the Blue Duck Reserve.

After collection soils were air dried and sieved through a 4 mm mesh. Propagating tubes were filled with soil and watered. Pots were placed on petri dishes to slow water and nutrient loss. Seedlings at the one true leaf stage were transplanted into treatments.

Nutrient Treatments. Phosphorus treatments were: 0 (distilled water) and NaH_2PO_4 5 x 10^{-3} M. Calcium treatments were 0 (distilled water), $CaCl_2$ 1 x 10^{-3} M and $CaCO_3$ 1 x $^{-3}$ M. Treatments were watered with nutrient solutions at weekly intervals.

4.2.5 Harvest

The transplant experiment was harvested after 130 days of growth, on the 18th February.

The shade experiment was harvested after after 63 days of growth on 28th of January.

Growth during winter months (June to mid-October) of plants in the soil moisture experiment was minimal despite artificial lighting which increased the photoperiod in winter to 9-30pm. Harvest was delayed until the 6th November, 160 days after transplanting.

The soil moisture content of each pot was determined using the method described in section 4.2.1..

The soil type and phosphorus and calcium addition experiment was harvested after 98 days growth on 3rd February.

Measurements. Plant height and number of leaves were recorded at harvest. Leaf areas were measured using a Delta-T Area Meter (Appendix 1). The shading experiment leaf areas were measured on a Li-Cor LI-3100 Area Meter. Dry weights of stems, leaves and roots were determined after drying to constant weight at 70 C.

4.2.6. Analysis

Transplant Experiment. Canonical correlation was carried out on data using the BMDP 6M program. The critical value of P was 0.1.

Analysis of variance was carried out on all other data in this chapter. The value of $P<0.05$ was used as the critical value for the analysis unless stated otherwise.

Planned Comparisons

Shade Experiment

1. 100% and 45% levels
2. 100% and 22% levels
3. 100% and 14% levels

Soil Moisture

1. Intermediate and Waterlogged
2. Intermediate and Drained

Soil Type and Phosphorus and Calcium

1. Beech soil and Podocarp soil
2. Beech soil and Broadleaf soil
3. Phosphorus Present and Absent
4. Calcium Present and Absent
5. $CaCO_3$ and $CaCl_2$

4.3 RESULTS

4.3.1. Transplant Experiment

The first canonical variable was most highly correlated with plant survival (R^2=0.53). The site conditions which describe the first canonical variable (Table 4.2) were low values of soil moisture and pH, an absence of litter and high values of PPFD. The second canonical variable was most highly correlated with plant height, number of leaves, leaf area and plant biomass (R^2=0.41). The site conditions which described the second canonical variable were presence of podocarp species and Macropiper excelsus, bareground, absence of a mid-canopy and ground layer species particularly grass species. The first and second canonical variables described the relationship between the establishment of C. vitalba seedlings and the site conditions at a significance level of $P<0.1$. Non significant values were excluded from results.

During the course of the fieldwork it was found that some of the light sensors were knocked off their posts and broken. The remaining sensors were still firmly attached with velcro. The cause of the damage was unknown; due to the inaccessibility of the site vandalism was unlikely. A more secure means of attaching light meters is required.

4.3.2. Light

Shade experiment. Shading significantly reduced shoot growth at the 14% light level. Root weight was significantly reduced at the 22% level. Leaf area showed a significant increase at the 22% level and decreased at the 14% level (Table 4.3).

Unshaded plants had red-purple pigmentation on leaves and stems. The 45% light treatment also had red pigmentation but to a lesser degree. Plants in the 14% light level had pale green leaves and stems. The 22% light treatment plants had leaves similar in appearance to the less shaded treatments, without red pigmentation (Fig 4.7).

Sun and Shade Leaves. Sun and shade leaves collected from the field showed no significant difference in leaf area. A significant difference was found between samples in

leaf weight and specific leaf area (SLA) (Table 4.4).

Scanning electron micrographs showed differences in morphology between sun (Fig 4.8) and shade (Fig 4.9) leaves. Leaves from shaded conditions are thinner. The palisade cells were shorter in length in shade leaves than those of sun leaves. In sun leaves palisade mesophyll cells were more tightly packed than in the shade leaves.

	CNVR1 $R=0.73$ $R^2=0.53$	CNVR2 $R=0.64$ $R^2=0.41$
Height	-0.003	0.464*
No. of Leaves	-0.054	0.571*
Survival	0.534*	0.407
Leaf Area	-0.105	0.894*
Leaf Wt	-0.041	0.787*
Stem Wt	0.026	0.863*
Shoot Wt	0.003	0.803*
Soil moisture 13 Oct 84	-0.410*	0.126
Soil Moisture 10 Dec 84	-0.354*	-0.003
Soil Moisture 14 Feb 85	-0.050	-0.115
pH	-0.400*	-0.068
Podocarp	-0.036	0.314*
Macropiper	-0.184	0.407*
Mid Canopy	-0.192	-0.323*
Open Ground	0.278	0.461*
Grass	-0.210	-0.319*
Litter	-0.576*	-0.396
% PPFD Oct	0.878*	0.131
% PPFD Feb	0.805*	0.260

Table 4.2 Canonical Analysis of the relationship between site characteristics and establishment of *C. vitalba*.

* Coefficients are those which were emphasized in the interpretation of the canonical variates.

% Total PPFD	Leaf Area cm^2	Leaf Wt (g)	Stem Wt (g)	Root Wt (g)	Total Wt (g)
100%	224.4 (15.0)	1.005 (1.227)	0.557 (1.028)	0.492 (0.996)	2.062 (1.436)
45%	278.2 (16.7)	1.160 (1.289)	0.628 (1.062	0.473 (0.948)	2.165 (1.471)
22%	#353.4 * (18.8)	#0.918 (1.191)	#0.638 (1.067)	#0.451 * (0.905)	#1.846 (1.359)
14%	168.2 (13.0)	0.292 * (0.890)	0.216 * (0.846)	0.369 * (0.756)	0.568 * (0.753)
(S.E. (n=6))	(1.09)	(0.07)	(0.04)	(0.02)	(0.10)
#(S.E. (n=5))	(1.19)	(0.08)	(0.04)	(0.02)	(0.10)
C.V.%	16.79	14.95	8.93	5.68	18.68

Table 4.3 Main effects of light level on leaf area and dry weight.

The data were transformed using square root transformation. (Transformed values in parentheses.)
* Significantly different from the 100% total PPFD treatment mean.
# Mean or S.E. include an estimated missing value. (Reduced degrees of freedom.)

Fig 4.7 Shade treatments (0=100%; I=45%; II=22%; III=14%).

Leaf Position	Leaf Area cm^2	leaf Wt. (g)	SLA (cm^2g^{-1})
Shade	73.21a	0.18a	432.08a
	(8.86)	(0.43)	(6.07)
Sun	73.27a	0.12b	217.02b
	8.56	(0.34)	(5.38)
(S.E.(n=10))	(± 0.4)	(± 0.03)	(± 0.03)
C.V.%	15.37	17.49	1.86

Table 4.4 Comparison of sun and shade leaves.

Data was transformed using square root (leaf area and weight) and natural logarithm (SLA). (Transformed means and S.E. in parentheses).

Means followed by the same letter are not significantly different (P>0.05) as determined by ANOVA.

Fig 4.8 Scanning electron micrograph of the internal structure of a sun leaf (Bar=50 μm).

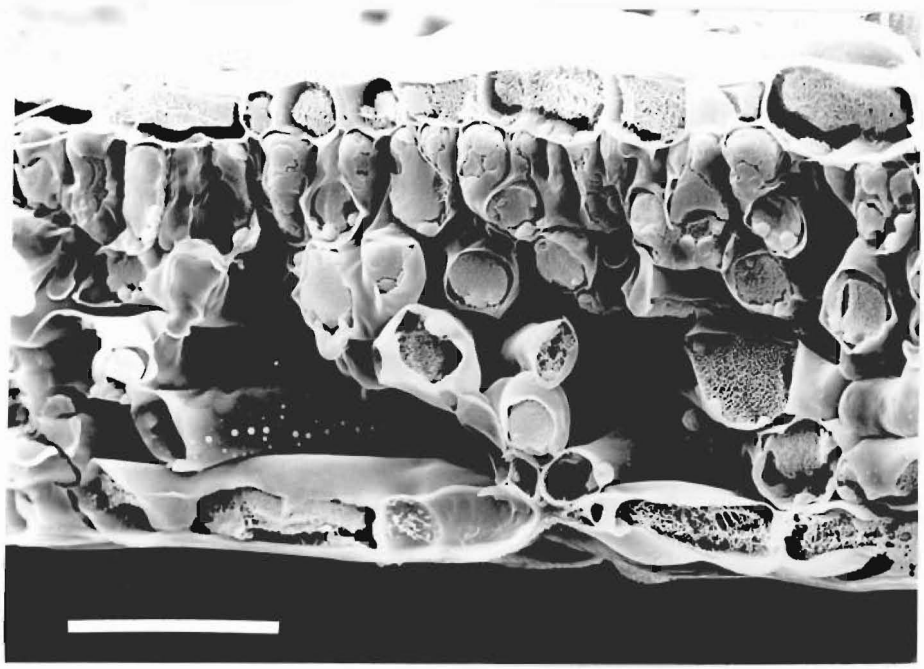


Fig 4.9 Scanning electron micrograph of the internal structure of a shade leaf (Bar=50 μm).

4.3.3. Soil Moisture

The simulation of different levels of drainage for treatments was successful. The effects of soil moisture content on plant growth are shown in Table 4.5. Total plant biomass (Fig 4.10) and leaf area (Fig 4.11) was significantly higher in the drained treatment. Stem weight was not affected by increased drainage from intermediate conditions. High soil moisture significantly reduced total biomass and leaf area.

The purple pigmentation of plants growing in the water-logged treatment (Fig 4.12) suggested they were possibly phosphorus deficient due to poor root growth. The soil of the water-logged treatments had a sulphurous odour suggesting soil was anaerobic. Plants in the other treatments had mid-green leaves and red stems.

4.3.4 Soil Type and Phosphorus and Calcium

The podocarp soil type was found by Duncan's Multiple Range test to significantly increase growth in *C. vitalba* ($P<0.01$). There was a large difference between results from podocarp soils and the other soils. As a result the data from the podocarp soil treatments were removed from the data set before final analysis. Calcium treatments were found to have no significant effect on growth. Due to heterogeneity of data between the calcium levels, all the calcium levels were pooled.

There was a significant interaction between soil type and phosphorus addition. Addition of phosphorus significantly increased total biomass (Table 4.6) and leaf area (Table 4.7) of seedlings in the beech soil. There was no significant difference between the phosphorus main effect means for biomass or leaf area. There was a significant difference between the soil types. Plants in the broadleaf soil had significantly higher leaf area and total biomass.

Plants in the beech soil with phosphorus added had less purple pigmentation than those without phosphorus. Addition of phosphorus did not appear to change colouration of plants in the broadleaf soil. Plants growing in the broadleaf soil had green-red pigmented leaves.

Soil Drainage	Stem Wt (g)	Leaf Wt (g)	Leaf Area (cm^2)	Root Wt (g)	Total Wt (g)	Moisture Content (%)
Drained	0.14	0.40 *	54.48*	0.26*	0.83*	7.71a
	(-1.98)	(0.202)	(7.38)	(-1.33)	(0.29)	
Intermed.	0.08	0.251	33.42	0.08	0.43	10.14b
	(-2.48)	(0.161)	(5.78)	(-2.50)	(0.21)	
Water Logged	0.02*	0.011*	2.49*	0.01*	0.05*	13.90c
	(-3.90)	(0.034)	(1.58)	(-4.90)	(0.07)	
(S.E. (n=10))	(±0.18)	(±0.01)	(±0.43)	(±0.20)	(±0.01)	(±0.63)
C.V. %	—	27.30	27.71	—	22.30	18.90
[a]Data Trans.	1	3	2	1	3	none

Table 4.5 Main Effects of Soil Moisture on plant dry weight and leaf area.

[a]The data were transformed using: 1. Natural logarithm; 2. Square Root; 3. Arcsine (x/10).
(Transformed values in parentheses.)
* Significantly different from the Intermediate treatment mean.

Moisture content means followed by the same letter are not significantly different ($P>0.05$) as determined by Duncan's Multiple Range test.

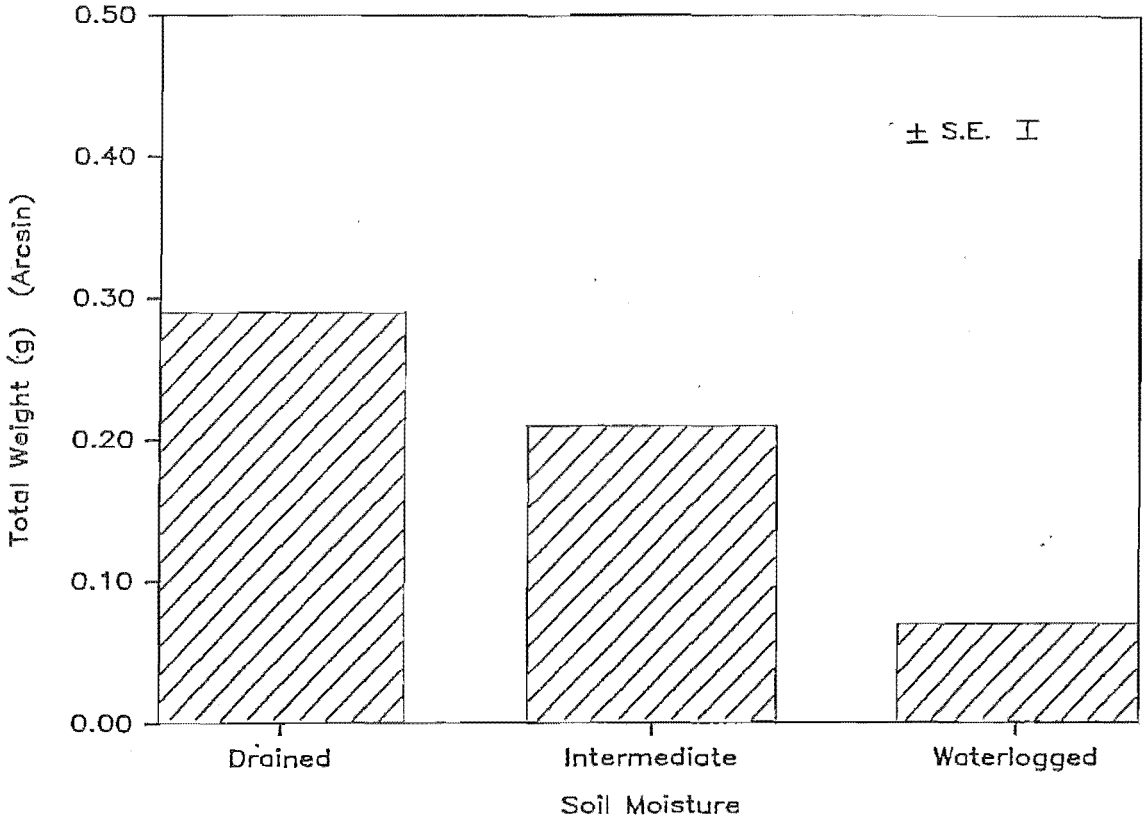


Fig 4.10 The effect of soil moisture content on total plant biomass.

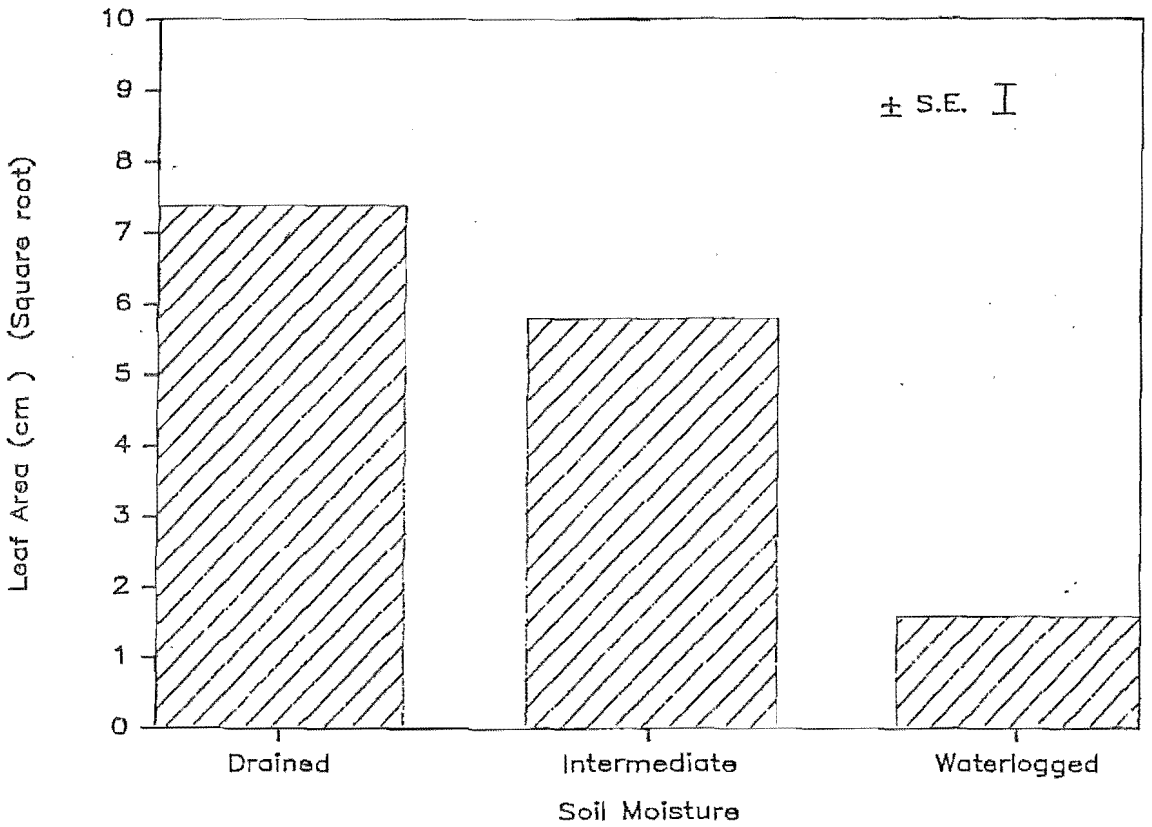


Fig 4.11 The effect of soil moisture content on leaf area.

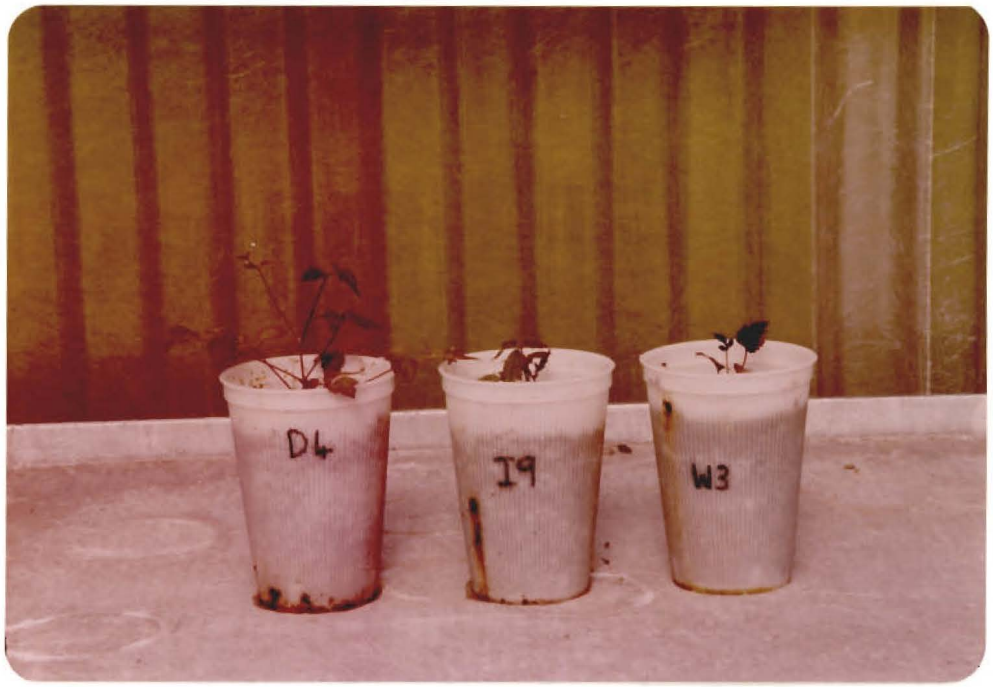


Fig 4.12 Soil drainage treatments (From left: Drained, Intermediate, and waterlogged).

Soil Type	Phosphorus		Soil Main Effect
	0	+	
Beech	0.014 (0.038)	0.034 (0.059)	0.023 (0.049)
Broadleaf	b 0.129 (0.115)	a 0.045 (0.068)	0.081 (0.091)
Phosphorus Main Effect	0.058 (0.077)	0.039 (0.063)	C.V.% =64.80

Table 4.6 The effect of soil type and phosphorus on total plant weight (g).
(Treatment S.E.= ± 0.01 (n=12); Main Effect S.E.= ± 0.01 (n=24)).
The data were transformed using arcsine (x/10) (Transformed values in parentheses).

Soil Type	Phosphorus		Soil Main Effect
	0	+	
Beech	2.44 (1.56)	4.73 (2.17)	3.50 (1.87)
Broadleaf	11.09 (3.33)	4.75 (2.18)	7.56 (2.75)
Phosphorus Main Effect	5.95 (2.44)	4.75 (2.18)	C.V.% =51.98

Table 4.7 Effect of soil type and phosphorus on leaf area (cm^2).
(Treatment S.E.= ± 0.35 (n=12); Main Effect S.E.= ± 0.25 (n=24)).
The data were transformed using square root. (Transformed values in parentheses.)

4.4 DISCUSSION

Transplant Experiment

The first pair of canonical variates seem to identify a relationship between plant survival and gaps. High values of percentage PPFD were correlated with high survival. To a lesser extent survival was associated with low values of soil moisture and pH and an absence of litter. Sites which were low in moisture and with low pH and an absence of litter tended to be those on open sites with no or little canopy cover. These sites also tended to receive higher levels of light. The low soil moisture, pH, and absence of litter are likely to be due to the exposure of the site. The disturbed site in the Blue Duck Reserve was the site at which the highest values of PPFD were recorded. The disturbed site soils were consistently drier throughout the growing season. The exposure of the site and lack of litter and organic material reduced its waterholding capabilities.

The second pair of canonical variates suggested a relationship between all the growth characteristics of C. vitalba seedlings and the vegetation of the sites. High rates of growth of C. vitalba occurred at sites associated with podocarp species and Macropiper excelsum, and sites which had large areas of bare ground and lacked mid-canopy and grass species. Macropiper excelsum was present at every site at which podocarp species occur. Three sites fit this description, the Puhi Puhi, Blue Duck podocarp and disturbed open canopy sites. These were the sites with the most bare ground, and no mid-canopy or grass species. Podocarp species were associated with all these sites.

The most important factor affecting establishment of C. vitalba is light. Results indicate that C. vitalba has a high light requirement for establishment. Forest types most susceptible to infestation are podocarp or podocarp-broadleaf forest types. In particular forest remnants, due to their small size, are susceptible to disturbances which allow weed species to become established.

Light. The amount of PPFD received significantly affected the growth of C. vitalba seedlings. This was demonstrated by the shading experiments under glasshouse

conditions, and from samples collected from the field. Shaded C. vitalba foliage showed morphological adaptations to shaded conditions.

Plants were not significantly affected by moderate levels of shading (45% treatment). However at lower light levels (14% total PPFD) total biomass was reduced. Tucker (1978) found that shading at 21% of total PPFD reduced root biomass by half and increased leaf area. The results in Table 4.3 show that although root biomass was significantly lower at the 22% level, it was not half that of the 100% level. Reduction of root weight in the 22% shade level was possibly due to decreased evaporative demand by shaded plants. The leaf area of plants in the 22% shade treatment was significantly higher than the unshaded treatment. Further shading caused a reduction in leaf area. This suggests that although C. vitalba has some ability to adapt to low light conditions it would still be limited to areas with at least 15-20% Of full sunlight. Measurements of percentage of total PPFD for the transplant experiment showed that under forest canopies total PPFD is usually less than 15%.

Seedlings in high light intensities tended to develop red pigmentation on leaves and stems. This was not present on plants at higher shade levels. The red pigmentation is possibly due to the production and accumulation of anthocyanins. Anthocyanins are thought to protect chlorophyll from destruction from ultra-violet radiation and are produced in response to high light intensity (Salisbury and Ross, 1979).

A comparison between sun and shade leaves which were growing naturally found morphological differences. The major difference was leaf thickness, the shade leaf in Fig 4.8 was 116.5 µm in thickness and the sun leaf in Fig 4.7 was 25% thicker (155.5µm). This would account for the differences in weight observed between sun and shade leaves. Although the leaf area was not significantly different between sun and shade leaves, shade leaves had significantly lower leaf weights. In low light conditions plants put more resources into light interception so leaves tend to be thinner. This maximises photon capture for the amount of

resources used in leaf tissue. Leaves are as thick as possible without having the lowermost cells too shaded by by other leaf cells. This maximises the number of cells with chloroplasts for a given investment in other leaf tissue.

The low growth rates at high levels of shading suggests that C. vitalba does not adapt fully to low light conditions. Only limited morphological changes were found in shaded plants growing in natural conditions. The light regime under which the shaded leaves were growing was not measured. However, measurement of forest light environments in the transplant experiment demonstrated how limiting PPFD is under a canopy.

Although recently germinated seedlings of C. vitalba were found in October at Kowhai Bush under the canopy, by December they had died. Other young plants growing under the canopy were found to be new shoots growing from old vine stems (Fig 1.3).

The results verify that the observation that C. vitalba is a light demanding plant. Establishment appears to be limited to canopy gaps and forest margins where the amount of light received is high.

Soil Moisture. The literature indicates that C. vitalba has a requirement for a free-draining soil. Ellenberg (1974) reported that C. vitalba in Europe occurs in aerobic soils with intermediate soil moisture. The response of plants to soil moisture was found to support this observation.

It was found that water-logging significantly reduced total biomass and leaf area. The purple pigmentation of leaves and stems indicated that plants were limited by phosphorus deficiency. Seedlings in the drained treatment showed a significant increase in total biomass and leaf area in comparison to the intermediate treatment. Plants in the intermediate treatment appeared smaller than those in the drained treatment but did not differ in pigmentation.

The restriction of C. vitalba to calcareous soils in moist climates is possibly due to physical soil factors rather than a requirement for calcium. Soils over chalk and limestone tend to be better drained (White, 1979) and this

would compensate for the wetter climate.

The distribution of C. vitalba in New Zealand at present is consistent with its requirement for a well-drained soil. It is notably absent from the western South Island which has both a high rainfall and gley soils with high moisture contents. However, it is present at Inangahua Junction on the banks of the Buller River. This indicates that establishment along river banks is possible as these alluvial soils tend to be free-draining.

Soil Type and Phosphorus and Calcium. The growth response of C. vitalba in the Blue Duck podocarp soil was highly significant compared to the other two soils. This suggests that soils from this forest type is more susceptible to invasion from C. vitalba.

C. vitalba growing on the broadleaf soil had significantly larger leaf areas and higher total biomass than the on the beech soil. Addition of phosphorus significantly increased growth on the beech soil. This indicates that the levels of phosphorus in the beech soil were low and that this may be a factor limiting growth of C. vitalba in this soil. A decrease in growth occurred in the broadleaf soil after addition of phosphorus. Gibbs and Beggs (1953) found this soil to have high levels of phosphorus. It is likely that levels of phosphorus in the broadleaf soil were optimum for growth and in balance with other nutrients. Addition of phosphorus possibly resulted in the supply of another nutrient becoming limiting, most likely nitrogen or potassium (White, 1979).

CHAPTER 5

STOMATAL PHYSIOLOGY

5.1 INTRODUCTION

The responses of a plant to the atmospheric environment are influenced by the stomata. Stomata control the rates of water loss and carbon gain of a leaf (Cowan, 1977). Optimal stomatal functioning will represent a compromise between these conflicting requirements for control of water use while maintaining an adequate level of carbon gain. Environmental factors which influence stomatal conductance include photosynthetically active photon flux density (PPFD), leaf water status, ambient humidity (vapour pressure deficit or VPD), leaf temperature, and carbon dioxide concentration. Difference in stomatal responses between species and ecotypes play an important role in plant adaptation to different environments (Hall et al.,1976).

An understanding of stomatal responses to the environment is required to determine how the environment affects photosynthesis and transpiration. Cowan (1977) and Cowan and Farquhar (1977) proposed that stomata act in such a way as to maximise carbon gain for a unit water loss. This ability to maximise assimilation for the amount of water used in transpiration has been defined as the water use efficiency (WUE) (Fitter and Hay, 1980). Stomatal responses to environmental factors will vary depending on the environment to which a plant is adapted. Plants growing in environments in which water may be limiting tend to have a higher intrinsic water use efficiency. In these environments plants tend to have a stronger response to decreases in atmospheric humidity (Schulze and Hall, 1982).

Plants growing on the forest floor are less likely to be limited by water availability. The evapo-transpirational demand is lower due to lower VPD, temperature and light regime than an exposed site. Transpiration is also lowered

due to higher boundary layer resistances. A high boundary layer resistance is caused by a relatively undisturbed layer of air at the leaf surface. Before entering the turbulent air above the leaf, the water vapour must diffuse through this boundary layer. The degree of resistance due to the boundary layer depends on wind velocity and leaf size and shape. Low wind velocity increases the size of the boundary layer. Large leaves have higher boundary layer resistances (Fitter and Hay, 1980).

The diurnal course of leaf conductance in plants growing under canopies has been found to follow that of light (Schulze and Hall, 1982). Where water is not limiting it has been shown that assimilation tends not to be limited by stomatal conductance (Cowan, 1977).

In the open due to higher evaporative demands, water can be more limiting to growth. Plants growing in open environments need to be able to control water loss in response to increased VPD. Response of stomata to humidity has been observed with virtually all species examined (Schulze and Hall, 1982). Stomatal response to humidity was described first in plants from desert habitats e.g. (Schulze et al., 1972) but it has also been observed in plants from most other habitats (Camacho-B et al., 1974; Johnson and Caldwell, 1976; Jarvis, 1980; Khairi and Hall, 1976). However the slope of the stomatal response to VPD varies with ecotype or the habitat to which the species is adapted. Plants from dry or open habitats tend to have a steep response to VPD while those from moist habitats tend to have a shallow response (Schulze and Hall, 1982).

The relationship between stomatal conductance (g_s) and the bulk water status of a plant or leaf is poorly understood (Schulze and Hall, 1982). However it has been shown in numerous studies that plants experiencing a degree of water stress have lower conductances than non-stressed plants. Measurement of 'pre-dawn' water potential can be used as an indicator of plant water status. High values of pre-dawn water potential indicate low water stress. The effect of variation of plant water potential depends on the length of time over which it occurs. A short term variation over one day has little effect on stomatal functioning and

as a result gas exchange. The long term variation was found to have more effect on gas exchange but not necessarily directly through the effects on stomata (Schulze and Hall, 1982). Measurement of pre-dawn xylem water potential gives an indication of a plants water status. The xylem water potential is closely related to soil water potentials in the root zone. Soil drought results in a decrease in pre-dawn xylem water potential and increased resistances to flow in the soil and plant. Measurement of mid-day water potential gives a value during the peak transpiration period of the day. This is the maximum water stress encountered by the plant during the day (Schulze and Hall, 1982).

Stomatal conductance tends to increase with photon flux. Conductance usually exhibits a hyperbolic response to photon flux (Burrows and Milthorpe, 1976). Schulze and Hall (1982) found that the photon flux required for 95% of maximal conductance varies substantially depending on the species, leaf age and preconditioning. Shade adapted foliage is characterised by low light saturation levels ($<500\ \mu molm^{-2}s^{-1}$), and a steeper initial response to increased light light intensity than sun foliage (Fitter and Hay, 1980).

Woods and Turner (1971) found that the rate of stomatal opening after transfer to higher light differed between shade tolerant and shade intolerant species. To open to a constant leaf conductance took 3 minutes in shade tolerant Fagus grandifolia (Beech) and 20 minutes in shade intolerant Liriodendron tulipifera (Yellow Poplar). With the rapid changes in light found in a forest, the ability of stomata to respond quickly to a sun fleck is an advantage. Rapid opening of stomata in shade tolerant species allows the species to take advantage of short periods of light for photosynthesis (Woods and Turner, 1971). Since most sunflecks have a short duration (Woodward, 1981) photosynthesis of shade intolerant species would be limited by stomatal conductance during brief sunflecks. Benecke et al. (1981) showed that stomatal conductance tends to be more limiting for photosynthesis in sun than in shade foliage.

Short term responses of conductance to a variable

environment results in a hyperbolic relationship between conductance and assimilation (Schulze and Hall, 1982). Farquhar and Sharkey (1982) suggest that to prove stomatal limitation of assimilation, it must be shown that as the rate of assimilation decreases as stomata close the internal carbon dioxide concentration (C_i), within the leaf, must also decrease.

Gas exchange was used to determine the ecological strategy of C. vitalba, in particular the stomatal response and assimilation rate at different photon flux densities. This gives an indication of the type of light regime to which C. vitalba is adapted. Stomatal response to VPD was measured to determine the ability of C. vitalba to control water loss. Taken together these might indicate areas susceptible to invasion by C. vitalba.

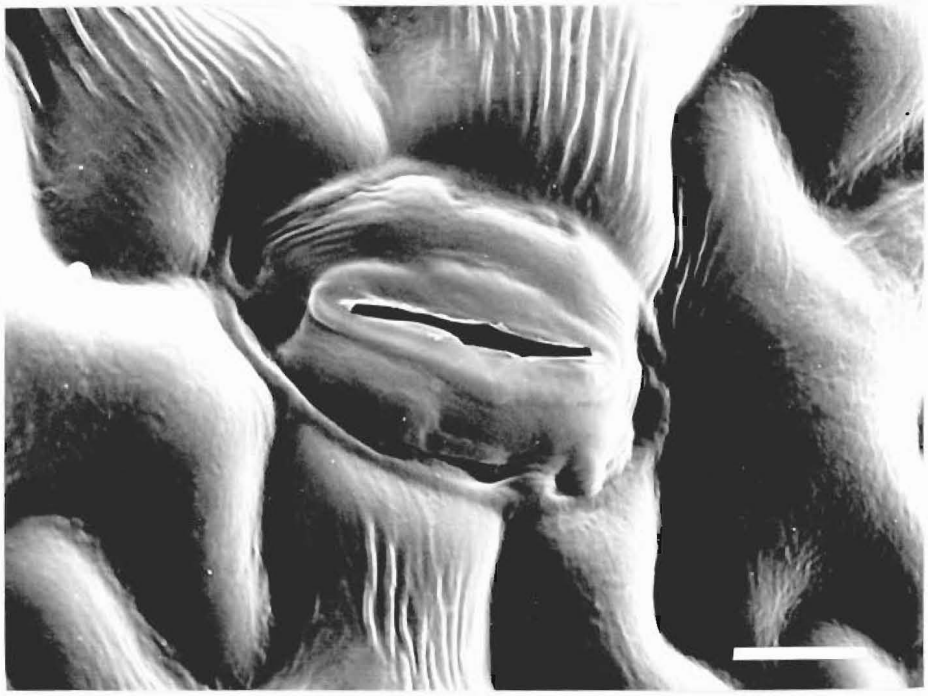


Fig 5.1 Stoma on the lower surface of a C. vitalba leaf (bar=10 μm).

5.2 MATERIALS AND METHODS

Gas exchange measurements were made on C. vitalba vines growing on native vegetation at Kowhai Bush, Kaikoura (description Chapter 4). Measurements were made during the 1984-1985 growing season over periods of a week in October, December and February.

The stomatal conductance and net carbon assimilation of plants was measured under ambient conditions. Plants in both full sun and shaded conditions were measured. Five consecutive measurements were made per leaf on fully expanded leaves. Leaves were sampled several times a day and were harvested at the end of the measurement period. The leaf areas were measured with a Delta-T Area Meter. Gas exchange was measured using a LI-Cor LI-6000 portable photosynthesis system, using a four litre polycarbonate chamber. Air in the chamber was mixed with two fans. Boundary layer resistance values and the calculation were obtained using a moist filter paper replicate of a C. vitalba leaf. The data were computed and analysed using programs written by Paul R. van Gardingen, University of Canterbury. Conductance and photosynthetic rates were compared at different ambient PPFD and vapour pressure deficits (VPD).

The xylem potential of leaves near those used for gas exchange was measured during measurement periods. The water potential of leaves was measured with a PMS pressure bomb (Scholander et al., 1965) (Appendix 1). Water potentials were measured at intervals before dawn (pre-dawn) and during the day.

5.3 RESULTS

A strong response was found between stomatal conductance and vapour pressure deficit (VPD) (Fig 5.1). Within any light interval there was stomatal closure with increasing atmospheric dryness. Stomatal response to VPD was more pronouced at higher light intensities. Stomatal conductance increased with increasing photon flux density. Stomatal opening became saturated at relatively high PPFD, around 1500-2000 $\mu molm^{-2}\ s^{-1}$. As the PPFD increased (Fig 5.2) the assimilation rate rose reaching saturation around 1500-2000 $\mu molm^{-2}\ s^{-1}$. When shaded leaves were transferred from low light (50 $\mu molm^{-2}\ s^{-1}$) to full light (2000 $\mu molm^{-2}\ s^{-1}$) it was observed that stomata took up to 20 minutes to reach a constant leaf conductance.

Assimilation rate (A) increased with increasing stomatal conductivity (Fig 5.3) producing a curvilinear relationship. The internal carbon dioxide concentration within the leaf, (C_i) was also affected by stomatal conductance (Fig 5.4). Within a light level, the internal CO_2 concentration decreased with decreasing stomatal conductance. The stomatal effect on CO_2 concentration was more pronouced at higher light intervals.

Water potential was not measured during October fieldwork but rainfall during this month was high suggesting that soil water was not limiting. In December the lowest mean mid-day xylem potential recorded was -1.52 mPa with a mean pre-dawn xylem potential of -0.24 mPa. In February the lowest mean mid-day xylem potential recorded was -1.95 mPa with a mean pre-dawn xylem potential of -0.24 mPa.

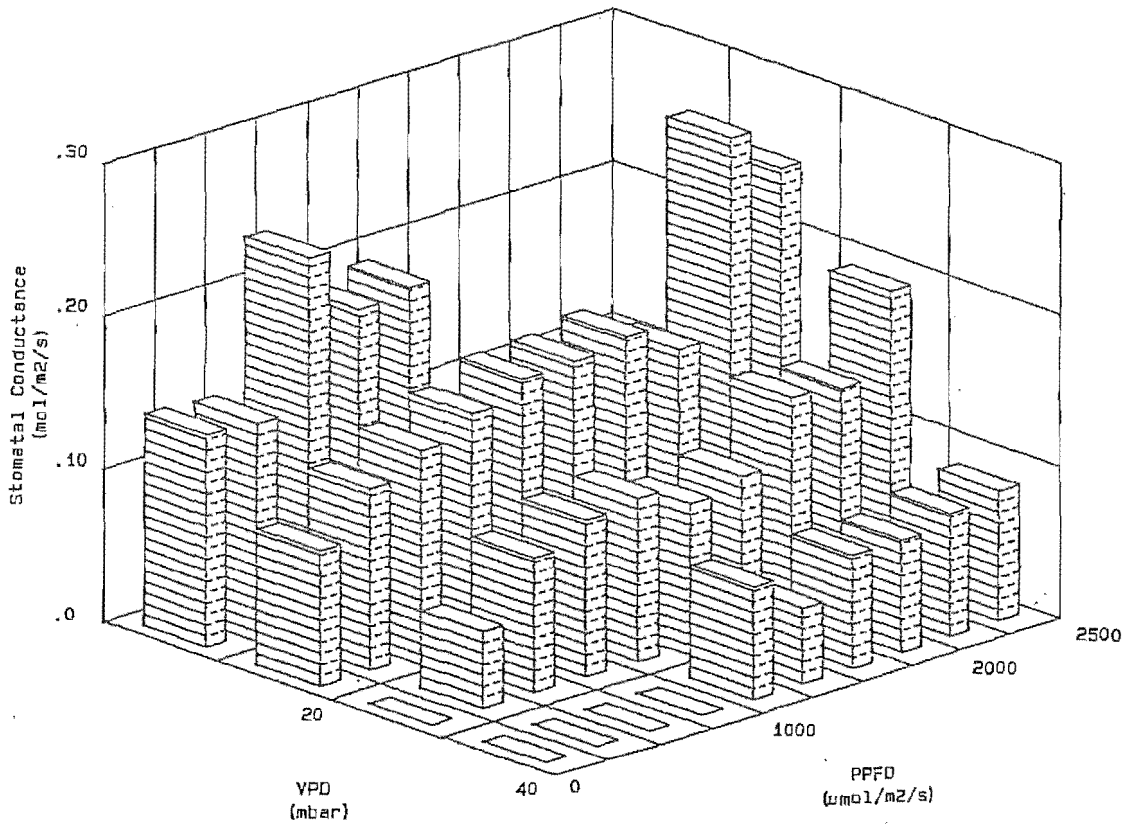


Fig 5.2 The effect of VPD and PPFD on Stomatal conductance in C. vitalba.

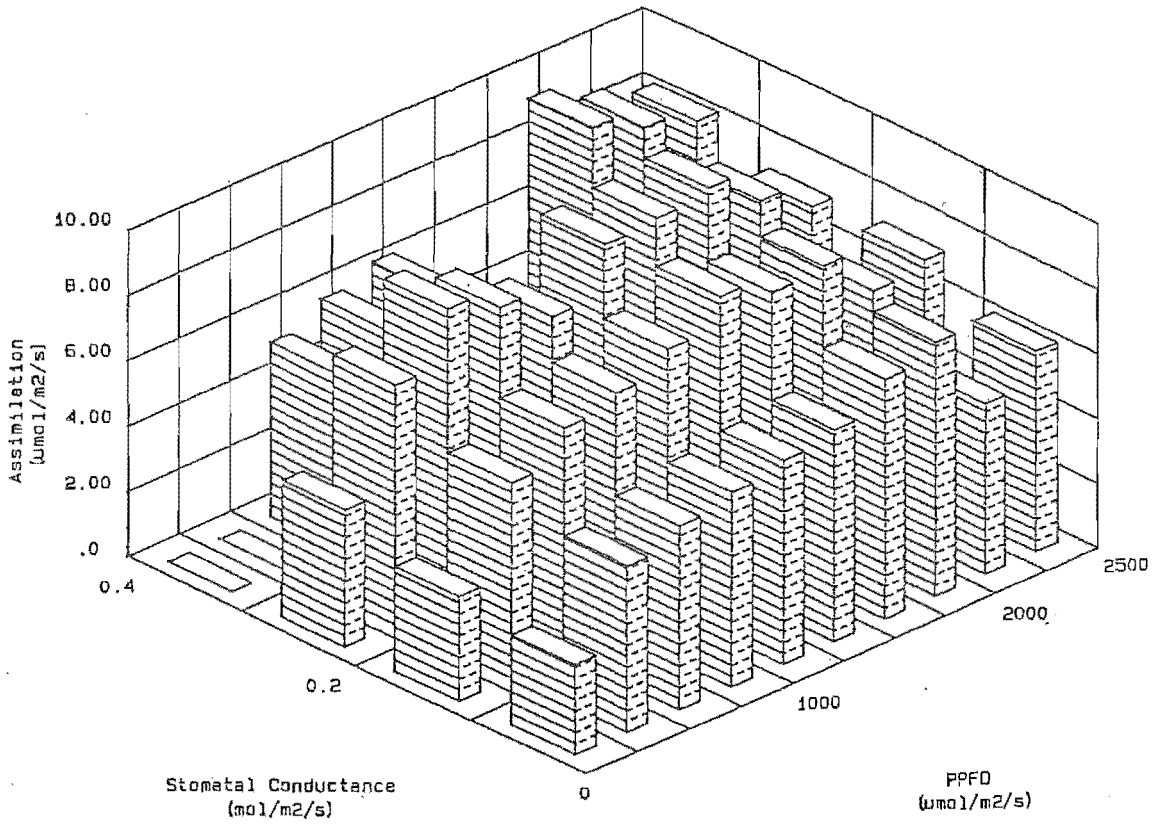


Fig 5.3 The effect of stomatal conductance and PPFD on assimilation in C. vitalba.

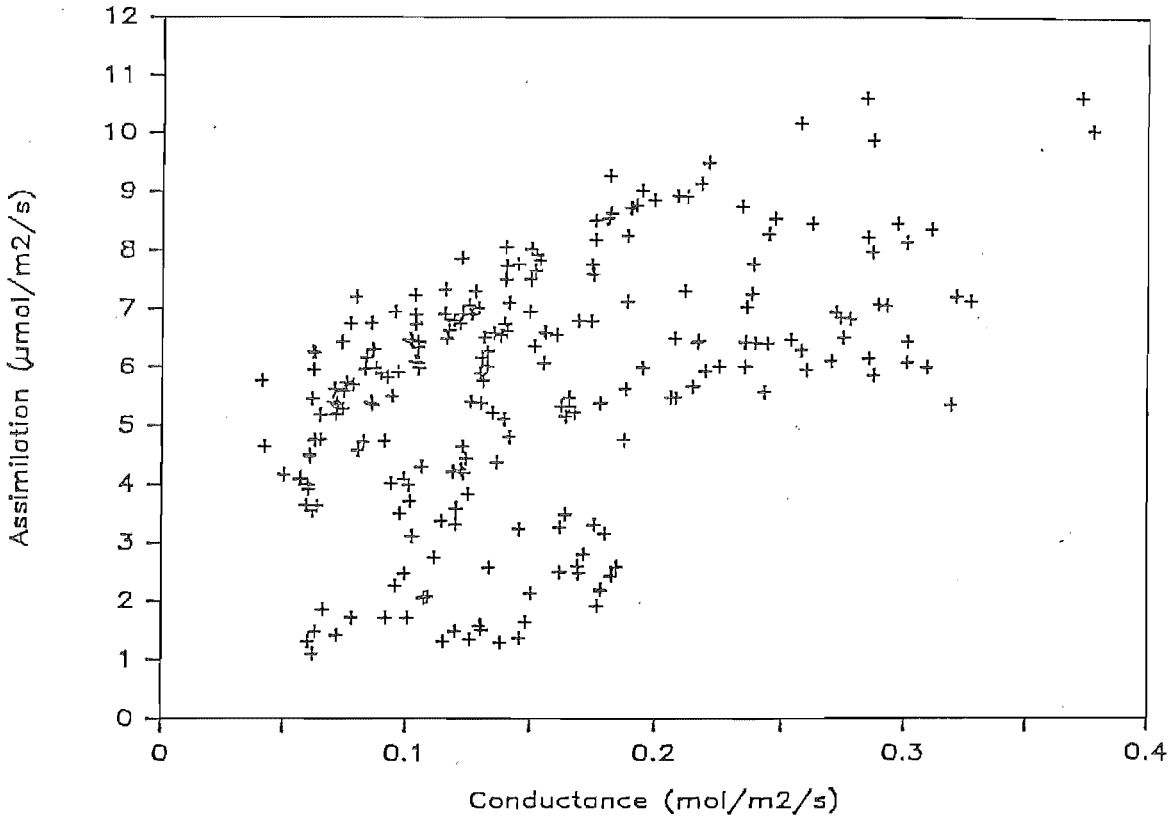


Fig 5.4 The relationship between stomatal conductance and assimilation in C. vitalba.

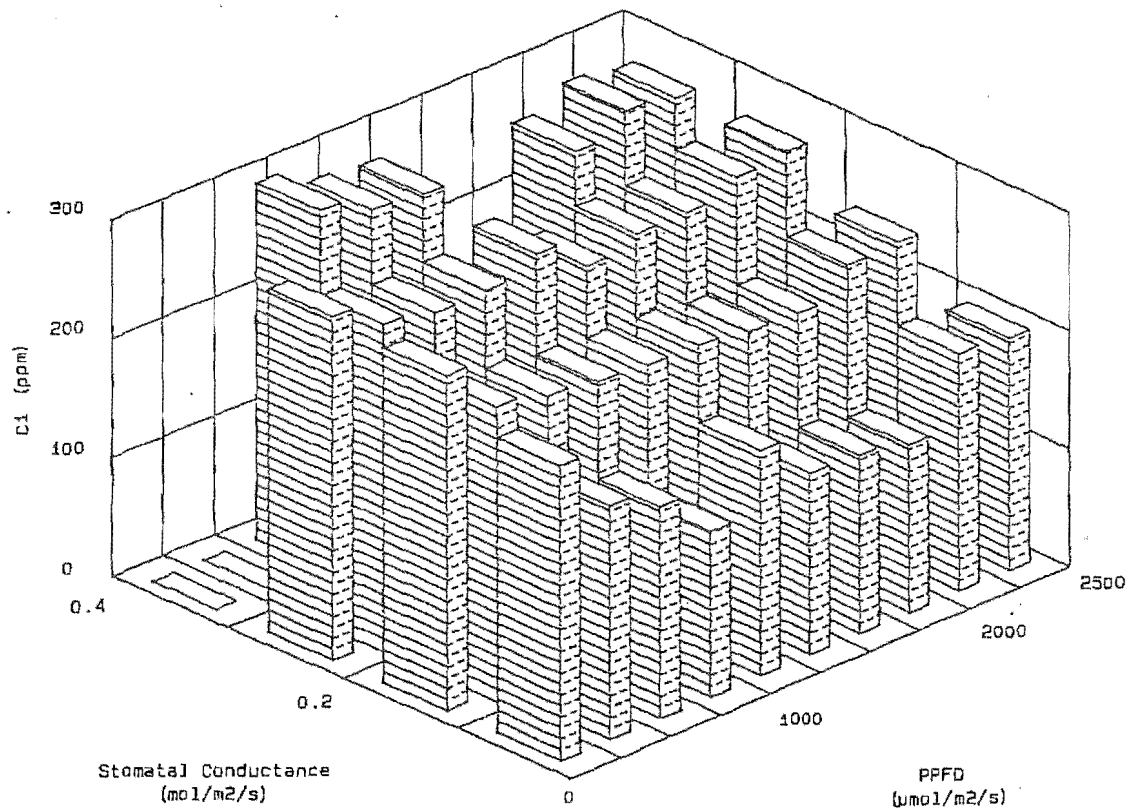


Fig 5.5 The effect of stomatal conductance and PPFD on the internal CO_2 concentration (C_i).

5.4 DISCUSSION

C. vitalba responds strongly to increasing atmospheric dryness with stomatal closure (Fig 5.1). A similar strong stomatal response to VPD has been shown for Sesamum indicum (sesame) (Camacho-B et al., 1974; Hall and Kaufman, 1975) and Capsicum frutescens (pepper) (Camacho-B et al., 1974) both species are adapted to arid environments. A strong response to leaf-air vapour pressure deficit (VPD) is a characteristic of sun adapted plants (Schulze and Hall, 1982). Xylem water potentials although reaching values of -1.95 mPa at mid-day had pre-dawn potentials of -0.24 mPa. This suggests that water potential was unlikely to reduce limiting stomatal conductivity as plants regained high values overnight.

The ability of C. vitalba to invade established forest would be dependent on its tolerance to shade. Growth of plants on the forest floor is more likely to be limited by light than by water availability. Absence of periods of high light intensity prevents light demanding plants from growing in shaded conditions. C. vitalba has a high light saturation value of 1500-2000 $\mu molm^{-2}$ s^{-1} for assimilation (Fig 5.2) and for stomatal conductance (Fig 5.3). Fitter and Hay (1980) describe high light saturation as being characteristic of sun adapted plants. Other vines have been demonstrated to have high light saturation values for assimilation and stomatal opening. Vitis vinifera (grapevine) (Friedemann and Smart, 1971; Kliewar et al., 1972) and Actinidia chinensis (kiwifruit) (I.J. Warrington, pers. comm.) were found to saturate at high PPFD.

High light saturation for stomatal opening and assimilation would be a disadvantage for C. vitalba vines growing in the shade, since species with high light saturation values tend to have a high light compensation point (Fitter and Hay, 1980). High rates of photosynthesis combined with low photosynthetic efficiency under low PPFD would combine to produce a low or negative carbon balance in plants under a canopy.

Stomatal opening in C. vitalba took 20 minutes to

complete after transfer from low to high light intensity. Assimilation of C. vitalba in the shade would be limited by stomatal conductance during brief sunflecks. Woods and Turner (1971) found a similar response in Yellow Poplar which they attributed to its adaptation to high light intensity and shade intolerance.

A strong correlation exists between stomatal conductivity and assimilation in C. vitalba (Fig 5.3), with low values of assimilation associated with low stomatal conductance. A decrease in the internal carbon dioxide concentration, within the leaf, (C_i) occurred with decreasing stomatal conductance (Fig 5.4). This concurrent decrease in C_i and assimilation with decreasing stomatal conductance is evidence that stomatal conductance limited photosynthesis in C. vitalba.

C. vitalba is usually found growing in disturbed sites and along forest margins (Atkinson, 1982). This suggests that C. vitalba requires high light intensity for successful establishment. The stomatal physiology of C. vitalba is characteristic of a light demanding plant with adaptations to minimise water loss. As a result it is unlikely that C. vitalba would establish and reach the canopy from under shaded conditions. In reserves with low infestations of C. vitalba, removal of seed sources and periodic checking of reserve margins could mean that further infestations would be prevented.

CHAPTER 6

MINERAL NUTRITION

6.1 INTRODUCTION

Information on the nutrient requirements of C. vitalba is sparse. Its association with calcareous soils in Britain has led to the suggestion that it has a high requirement for calcium (Salisbury, 1921). Salisbury (1952) records C. vitalba as occurring on a wide variety of soils, in particular, those rich in bases. Mitchell (1975) suggested that due to its abundance on alkaline soils C. vitalba requires a soil with a high base status.

Tucker (1979) studied the growth response of C. vitalba seedlings watered with solutions lacking essential nutrients. The nutrient solutions used lacked phosphorus, nitrogen, sulphur, iron, magnesium, calcium, or potassium. The control was a complete nutrient solution. It was found that lack of nitrogen, potassium and sulphur decreased total biomass. Plants watered with the solution lacking calcium died.

Calcicole species are described as having a high requirement for calcium and a sensitivity to toxic ions such as aluminium (Bannister, 1976). On the basis of the results of Tucker (1979) C. vitalba appears to fit the description of a calcicole species.

In Britain and Northern Europe the calcicole species are often plants which are at the northern limit of a more general distribution in Central and Southern Europe. Sankey (1966) reports that on the Continent C. vitalba tolerates a wide range of soils. Ellenberg (1974) lists C. vitalba as occurring mostly in neutral soils, but also in acidic and basic ones.

The soil pH affects the solubility of many soil minerals. Their solubility may be increased to such an extent that they become toxic. Aluminium and iron increase

in availability with decreasing pH. There is also a strong relationship between the amount of calcium in the soil and its pH. This has resulted in a tendency to term all plants from soils with a high pH as calcicolous (Bannister,1976).

The effects of calcium may be independent of pH. Clarkson (1965) experimented with calcicole and calcifuge species of Agrostis. A. tenuis, A. stolonifera, and A. canina all showed an increase in root growth with calcium sulphate addition without a change of pH. In contrast the calcifuge species A. setacea showed no response to addition of calcium. Other experiments involving Agrostis species have shown a range of tolerance to Aluminium. A. setacea (the calcifuge species) was tolerant to aluminium. A. canina and A. tenuis showed an intermediate response. The calcicole species A. stolonifera was the least tolerant (Clarkson, 1966).

The study was to determine whether C. vitalba has a high requirement for calcium or whether pH is more important in determining its distribution. The effect of iron and aluminium on the growth of C. vitalba was also examined. The absence of C. vitalba from low pH soils may be due to iron or aluminium sensitivity. Many calcicole species are not tolerant of these metal ions. Agrostis tenuis has a known response to the calcium, pH, and aluminium treatments. For this reason it was used as a control for the experimental system.

6.2 MATERIALS AND METHODS

Sand Culture

The effect of selected minerals on the growth of C. vitalba and A. tenuis was examined. A 2:1 mix of white quartz sand and pumice was used as an inert media. The sand was cleaned acid washing in 5% Hydrochloric acid for 48 hours, followed by four to five days leaching with water. A tube with small holes punched at regular intervals, was placed in the bottom of a 20 litre plastic bucket. Sand was placed on top of the tube and tap water passed through the tube. This process was carried out in a glasshouse until the pH of the sand eludate was neutral.

The sand and pumice mix was put into the individual pots and leached again for two weeks by the glasshouse watering system and trickle feed irrigation.

Seedlings

C. vitalba. Seeds were pretreated for 3 days with 10^{-4} M GA_3 and then sown in a flat seedling tray. Seedlings were transplanted at the two leaf stage to individual 7 cm pots containing the sand and pumice mix.

Agrostis tenuis. Seeds of A. tenuis were sown one week later than C. vitalba seeds into seedling trays and transferred into treatments as for C. vitalba.

IRRIGATION SYSTEM

The watering system in the glasshouses was not suitable for watering sand culture due to leaching. A trickle feed irrigation system was constructed for the sand culture experiments.

The overhead watering outlets at the rear of one glasshouse were sealed over two benches. The area was partitioned using clear sheets of polythene. Black polythene hose was used to construct the trickle feed system. This consisted of three hoses for each of the two benches connected to a supply hose. A flow restriction valve was fitted to the supply hose to reduce the rate of irrigation. Flow rate was further reduced by 25 cm long, 0.5 mm trickle feed tubes. Tubes were placed in the hose at 12 cm intervals.

Trickle feed tubes were placed in each pot from the top so that the outlet was at the midpoint in the pot. This allowed water to be supplied with minimal leaching of the added nutrients. Petri dishes were placed under each pot to prevent mixing between treatments.

6.2.1. Calcium and pH

Calcium Treatment Solutions. A two factor experiment was designed to examine the effect of calcium and pH on the growth of C. vitalba and A. tenuis. The calcium requirement for most plants in nutrient solutions is thought to be approximately 5 x 10^{-3} M (Hewitt, 1966). C. vitalba is thought by many to be a calcium requiring species. To test for this requirement higher concentrations were included. Treatments consisted of five levels of calcium and two pH levels. Calcium was supplied as $CaCl_2$ at concentrations of 0 (distilled water), 5 x 10^{-4} M, 5 x 10^{-3} M, 5 x 10^{-2} M and 5 x 10^{-1} M. These were watered weekly with 10 ml of the corresponding solution.

At the same time treatments were watered with 10 ml of the pH 3.6 or 5.6 buffered nutrient solutions minus calcium (Appendix 3). The buffer selected needed to be neutral and provide no extra nutritional source. For this reason a sodium acetate/acetic acid buffer was used.

6.2.2. Iron Sensitivity

The effect of iron on C. vitalba and A. tenuis was determined by the addition of different concentrations of iron, supplied as $FeSO_4$ at four levels. The four levels of $FeSO_4$ were : 0 (Distilled water), 5 x 10^{-5} M, 5 x 10^{-4} M, and 5 x 10^{-3} M. Iron is usually supplied at 1 x 10^{-4} M in micronutrient solutions (Hewitt, 1966). Essential nutrients were supplied as listed in appendix 3. The treatments were watered as for the previous experiment.

6.2.3. Aluminium sensitivity

The effect of aluminium on C. vitalba and A. tenuis by addition of aluminium at different concentrations. The aluminium was supplied as $Al_2(SO_4)_3$ at four levels. The four levels were : 0 (distilled water), 2 x 10^{-4} M, 4 x 10

$^{-4}$ M, and 8 x 10^{-4} M. Essential nutrients were supplied as given in appendix 3. The treatments were watered as for the previous experiment.

6.2.4. Harvest

All the sand culture experiments were harvested after 15 weeks of treatment. Leaf areas of C. vitalba were determined using a Delta-T area meter. Total plant weight of C. vitalba and shoot weight of A. tenuis was determined after drying to constant weight in an oven at70 C. A. tenuis root weight was excluded from the measurements as roots could not be extracted successfully from the growing media.

Analysis. Analysis of variance was carried out on data. The critical value of P was taken as 0.05 for the analysis.

6.3 RESULTS

6.3.1. Calcium and pH

A. tenuis shoot weight showed no response to increasing concentrations of calcium or pH (Table 6.1 and 6.2). There were no apparent differences in appearance of plants between treatments. C. vitalba total weight and leaf area showed no significant difference between the pH levels and calcium concentrations (Table 6.1 and 6.2).

6.3.2. Iron Sensitivity

The response of A. tenuis shoot weight (Table 6.3) to increasing levels of iron was not significant. There was no significant response of C. vitalba total weight or leaf area (Table 6.3). Most of the A. tenuis plants showed signs of chlorosis. There was only slight evidence of chlorosis in plants of C. vitalba.

6.3.3. Aluminium Sensitivity

There was no significant difference in the shoot weight of A. tenuis (Table 6.4) between treatments. C. vitalba (Table 6.4) showed no significant response in leaf area or total weight to increasing levels of aluminium.

	C. vitalba		A. tenuis
Calcium Conc. (M)	Total Wt (g)	Leaf Area (cm^2)	Shoot Wt (g)
0	0.47	22.51	2.60
5×10^{-4}	0.32	19.75	1.88
5×10^{-3}	0.34	14.82	2.59
5×10^{-2}	0.42	26.9	2.60
5×10^{-1}	*0.22	*9.53	2.90
S.E.(n=6)	± 0.1	± 4.9	± 0.4
*S.E.(n=3)	± 0.1	± 6.9	
C.V. %	55.63	63.54	40.73

Table 6.1 Main effects of calcium on the growth of C. vitalba and A. tenuis.

* Mean or S.E. includes estimated missing value or values. (Reduced Degrees of Freedom.)

	C. vitalba		A. tenuis
pH	Total Wt (g)	Leaf Area (cm^2)	Shoot Wt (g)
3.6	0.378a	20.05a	2.77a
5.6	0.327a	17.36a	2.27a
S.E.(n=15)	± 0.1	± 3.2	± 0.3
C.V. %	55.63	63.54	40.73

Table 6.2 Main Effects of pH on the growth of C. vitalba and A. tenuis.

Means followed by the same letter are not significantly different as determined by ANOVA.

	C. vitalba		A. tenuis
Iron Conc. (M)	Leaf Area (cm^2)	Total Wt (g)	Shoot Wt (g)
0	22.77	0.51	2.20
5×10^{-5}	24.57	0.46	1.90
5×10^{-4}	26.67	0.50	2.08
5×10^{-3}	28.02	0.45	2.28
S.E.(n=5)	± 5.00	± 0.08	± 0.46
C.V. %	43.82	39.50	48.19

Table 6.3 Main Effect of Iron on the growth of C. vitabla and A. tenuis.

* Significantly different from the 0 Iron Treatment Mean.

	C. vitalba		A. tenuis
Aluminium Conc. (M)	Leaf Area (cm^2)	Total Wt (g)	Shoot Wt (g)
0	18.04	0.36	1.82
2×10^{-3}	17.74	0.34	2.05
4×10^{-3}	11.55	0.21	2.11
8×10^{-3}	18.10	0.35	1.40
S.E.(n=5)	$\pm$ 3.5	$\pm$ 0.07	$\pm$ 0.41
C.V. %	48.17	46.41	49.17

Table 6.4 Main Effects of Aluminium on the growth of C. vitalba and A. tenuis.

* Significantly different from the 0 Aluminium Treatment Mean.

DISCUSSION

A. tenuis (the control plant) showed no response to increasing calcium concentration. Clarkson (1965) found an increase in shoot weight with calcium addition until the concentration in the medium exceeded 2.5×10^{-4} M. At this concentration there was no significant increase in shoot weight. The lowest calcium concentration used in this study was 5×10^{-4} M. However a significant increase in shoot weight would have been expected between the 0 calcium treatment and the 5×10^{-4} calcium treatment if the experimental system was working.

There are no data available for the response of A. tenuis to increasing iron concentrations. It would be expected that an absence of iron would produce iron deficiency symptoms of chlorosis of leaves. All the treatments had leaf chlorosis, even those which included iron.

Clarkson (1966) reported that shoot weight of A. tenuis decreased slightly with concentrations of aluminium above 2×10^{-4}. A. tenuis was described as having an intermediate tolerance to aluminium. The concentrations of aluminium used in this experiment were the same as those used by Clarkson (1966). The response of A. tenuis grown in sand culture to increasing concentrations of aluminium was not significantly different.

C. vitalba showed no response to any of the applied treatments. In appearance plants were stunted and showed signs of nutrient deficiency.

These results indicate that there may have been a failure in the experimental system. It is possible that the rate of flow of water through the trickle feed system was too fast. This would have caused a rapid loss of the added nutrients from the system. As a consequence neither species was subjected to treatments long enough to respond.

The usefulness of sand culture for nutrition experiments is limited. Unless a means of continuously supplying nutrients is available it should not be used. A continuous water supply, such as a trickle feed system, is

necessary for plants growing in sand as drainage is rapid. However, this type of water supply tends to rapidly leach added nutrients from the system. Other types of media may contain impurities particularly micronutrients. These may be of use for macronutrient studies. Water culture is often limited by the species used, plant species requiring good drainage are not usually suitable.

CHAPTER 7

CONTROL METHOD

7.1 INTRODUCTION

In South-Western Europe where C. vitalba originates it is not considered a serious weed. Its conservation in Britain is recommended by Mitchell (1975) for its attractive appearance and use as a habitat by various insect, bird, and small mammal species. C. vitalba is a problem in young forestry plantations in Britain (Mitchell, 1975) and conifer plantations in Germany (Ehlers, 1965). Vineyards in France that practice zero-tillage using 2,4-D and simazine for weed control also have problems with C. vitalba (Fort, 1975, 1979).

Various types of herbicides have been tested for control of C. vitalba and other Clematis species with conflicting results. Rooted cuttings of ornamental Clematis species were found to be resistant to simazine (van de Laar, 1967). Fryer and Makepeace (1978) found C. vitalba to be moderately susceptible to a leaf spray of 2,4,5-T. C. vitalba was not affected by winter or summer treatment of 2,4,5-T or 2,4,5-T and 2,4-D applied as an invert emulsion with 10% fuel oil (Harranger et al., 1964). Pecheur (1967) had little success spraying cut stumps of C. vitalba and the surrounding ground with 2,4,5-T at 40 kg/ha in 200 l of water. Addition of 2,4-D or 2,4-D and diesel oil did not improve results. A later application, 1-2 months after cutting, of 15 kg 2,4,5-T and 2.5 kg Picloram gave good control. Ehlers (1965) found C. vitalba to be resistant to amitrole and dalapon applied as a spray between early June and mid-July in conifer plantations in Germany. Control was obtained by Fort (1975) using amitrole in vineyards. Matthews (1975) found application of 2,4-D and picloram as a leaf spray gave good control.

Other species of Clematis have been controlled using

herbicides. C. orientalis was reported by Ivon Watkins Dow Ltd (1971) to be controlled with a leaf spray of 2,4,5-T and picloram. Skroch et al. (1975) used terbacil for weed control in apple orchards in the USA and found only an increase in the amount of C. virginiana present. The Department of Lands and Survey in New Zealand controls C. vitalba vines by cutting at ground level and waist height then treating cut ends with 2,4,5-T and diesel (Popay, 1982).

In New Zealand a method is needed that will control infestations of C. vitalba without serious damage to the native vegetation. Many of the serious infestations are in remnants of lowland forest. These lowland forest areas are particularly at risk to serious damage because of their small size and modified condition (Esler, 1978; Healy, 1969).

A technique used by Takayuki Isokaura et al. (1973) in which picloram impregnated 15 cm wooden needles were used to kill Kudzu vine was tested on C. vitalba. The technique was tested using various herbicides chosen for their ability to be translocated and for past effectiveness on other woody species.

7.2 MATERIALS AND METHODS

7.2.1 Herbicides Chosen

Dicamba. 3, 6-dichloro-o-anisic acid is a benzoic acid herbicide with similar structure to the broad-spectrum herbicide 2,3,6-TBA. The difference in structure is a replacement of the chlorine in 2,3,6-TBA in the 2 position with a methoxy radical. This change is sufficient to improve selectivity (Kearney and Kaufman, 1969).

Dicamba is formulated in the liquid form as the dimethylamine salt. It is used for the control of broadleaf weeds and woody plants not controlled by phenoxy herbicides. Dicamba is translocated in both the apoplastic and the symplastic systems (Klingman et al., 1982). It has been found to be excreted by roots into the surrounding soil or medium (Linder et al., 1964; van den Born and Chang, 1967;

Foy and Hurtt, 1965, 1967). It is persistent in soil and phytotoxicity may remain for several months. Application of Dicamba is by spray, or for woody plants it can be injected (Klingman et al., 1982).

Glyphosate. N-phosphonomethyl glycine is used as a herbicide in the form of the monoisopropylamine salt. Glyphosate is a non-selective, broadspectrum herbicide which is effective on most herbaceous plants. It also controls many woody brush species. Glyphosate has a high mobility and moves via the symplast and probably later in the apoplast (Klingman et al., 1982).

2,4,5-T. 2,4,5-trichlorophenoxyacetic acid belongs to the auxin herbicide group. this group also includes 2,4-D and derivatives of picolinic acid such as picloram (Ashton and Crafts, 1973). 2,4,5-T is effective on many woody species that are resistant to 2,4-D. Formulation is usually as amine salts which are water soluble or as esters which are oil soluble and usually emuslifiable in water (Klingman et al., 1982). Translocation in the plant is largely in the phloem (Salisbury and Ross, 1978).

Picloram. 4-amino-3,5,6-tichloropicolinic acid. Picloram is an extremely mobile compound, readily absorbed by foliage and roots and translocated in both the phloem and the xylem. It is particularly effective against woody species (Ashton and Crafts, 1973).

7.2.2 Field Application

The technique used was similar to that described by Takayuki Isokaura et al. (1973) for control of Kudzu vine. Wooden masonry plugs, 15 mm in length, were soaked in the concentrated herbicide solutions for 24 hr. Herbicides used were glyphosate (Roundup, Monsanto), dicamba (Shell), a 2,4,5-T ester (Broadside, Shell) and a mixture of 2,4,5-T and picloram (Tordon 520, Ivon Watkins Dow).

Permission was obtained from the Marlborough Catchment Board, Kaikoura to apply herbicides to C. vitalba vines in the Kowhai Bush River Protection Reserve using this technique. Kowhai Bush was selected as the experimental site due to the heavy infestation of C. vitalba at the eastern end.

In December, vines with stems of at least 2 cm diameter were chosen and holes were drilled in stems with a hand drill. A herbicide impregnated plug was inserted in the hole. three stems were treated for each plant. The vines were checked after two days and after two months and observations recorded.

7.2.3 Glasshouse Application

Seeds of C. vitalba were sown after treatment with GA_3 10^{-4} M for three days. Seedlings were transplanted in to 9 inch pots at the 3 leaf stage. This process was repeated 6 months later with a second batch of seedlings. After 12 and 6 months respectively, herbicide treatments were applied.

Herbicides used were the same as those used in the field experiment. In an attempt to simulate the field application method, on stems too small in diameter to drill, concentrated herbicides were applied to four replicates each of both 6 and 12 month old plants on 16/3/85. A short cut was made at approximately a 15^{o} angle into the stem. Herbicide was then painted on the cut using cotton wool soaked in concentrated herbicide. The control for the experiment was distilled water applied in the same manner. Observations were made at 1, 2, 6, 28, 49, and 70 days after application.

Fig 7.1 Stem of C. vitalba showing splitting after treatment with 2,4,5-T.

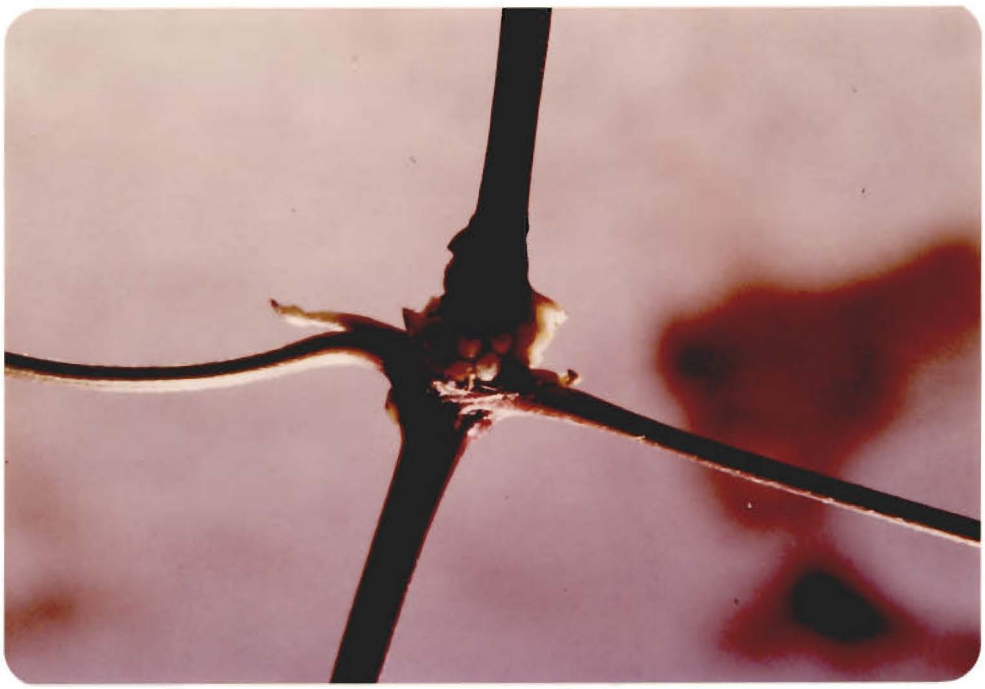


Fig 7.2 Proliferation of bud primordia at a node after treatment with dicamba.

7.3 RESULTS

7.3.1 Glasshouse Application

Control plants which were notched in a similar manner to the treated plants showed no adverse effects to the treatment.

2,4,5-T. The six month old plants treated with Broadside responded rapidly to the treatment. After two days plants were shriveled from the apex to the fourth node down. After six days the stems were twisted and epinastic effects were evident. Stem epidermis and phloem tissue were splitting after 28 days (Fig 7.1). By 49 days after application all plants were dead. The 12 month old plants took longer to respond. After 28 days some epinastic effects were visible and new growth had suppressed internodes and by 49 days plant tissue was browning. After 70 days all plants had died. All the plants treated with 2,4,5-T died.

Dicamba. The six month old plants responded rapidly, after one day plants were shriveled and epinasty was evident. After two days stems were twisted and by 28 days apices were dead and the purple pigmentation usually present in stems had gone. The epidermis of the stems were split and had a 'bubbled' appearance and nodes had developed a proliferation of bud primordia (Fig 7.2). Leaves had become chloritic. After 49 days two of the four plants were dead. The two remaining plants at 70 days were showing signs of recovery. These plants had malformed leaves and a proliferation of new shoots at nodes. The 12 month old plants were slower to respond. After 28 days leaves had become chloritic and by 70 days all of the plants had deformed leaves, and apices were dying back. New shoots had been produced by two plants from below ground level that showed no effects from the treatment.

Glyphosate. The six month old plants responded after six days from application with blackening of the apices. After 28 days the plants had continued to die back from the apex. After 70 days two of the plants were dead. The other two plants recovered but new shoots in the leaf axils had suppressed internodes. The new leaves which were produced

had narrow blades. All the 12 month old plants survived but responded in the same manner as the six month old plants 28 days after treatment.

2,4,5-T and Picloram Mixture. The six month old plants were limp and epinastic after one day, after six days the epidermis had split. By 28 days stems had lost pigmentation and leaves had become chloritic, apices were dead and basal leaves 'browning'. by 49 days all six month old plants were dead.

The 12 month old plants were slower to respond, after 28 days leaves were chloritic and the plants epinastic. After 49 days two plants were dead and the other two recovered.

7.3.2 Field Application

Since the vines to which herbicides were applied in the field differed in size, assessing the response was difficult. Herbicides were applied on 12 December and results assessed 3 days later and on 20 February, 70 days after application.

2,4,5-T had little effect on large vines which consisted of many stems. Leaves were deformed but growth continued. A smaller vine treated with 2,4,5-T died.

The response to the 2,4,5-T-picloram mixture was rapid. Total death had occurred after three days. No new shoots had appeared after 70 days. Response to dicamba was also rapid. One plant had died 3 days after treatment. Other vines, although consisting of many stems, were almost dead when examined in February. Glyphosate treated vines were seriously damaged but not dead in February.

7.4 DISCUSSION

The response of plants in all treatments was consistent with the symptoms of toxicity described in the literature.

Small glasshouse grown plants were highly susceptible to 2,4,5-T treatment. Response was rapid and all plants died. Large plants in the field showed less response to 2,4,5-T application. Some deformation of leaves occurred but the plants were not seriously affected.

The initial response of plants in the glasshouse to dicamba was rapid and resulted in serious damage. However, recovery occurred after a short time. Plants in the field also responded to treatment. Results from the glasshouse experiment suggest that plants in the field may eventually recover depending on the dose given.

Despite leaf deformation, the majority of glyphosate treated plants in the glasshouse recovered. In the field deformed leaves were still being produced three months after application. Information from the glasshouse experiment suggests that these plants may also recover.

The 2,4,5-T-picloram mixture killed young plants in the glasshouse. Older plants were found to be more resistant. The 2,4,5-T-picloram mixture was the most effective herbicide in the field treatments. Death was rapid and no signs of recovery were evident after two months.

The herbicide impregnated wooden plug was found to be an effective means of herbicide application. New growth on living vines, continued to be badly malformed two months after application.

Application of plugs would be faster than the current method of cutting and painting vines. Impregnated plugs in this study were used while still wet. The speed and safety of application would be improved by using dry plugs and a battery powered electric drill. However drying of plugs might also reduce the herbicide dose and its effectiveness. Battery drills and herbicide pastes have been used to control willows in Taranaki (Kelly, pers. comm.)

Further study should be made into ways of improving

this method of application. The minimum concentration of herbicide required and number of plugs needed per vine should be determined. Undiluted herbicides were found effective but damage to tissue at the point of application may impede transport. Dilution of herbicide might prevent or delay this from occurring and also reduce cost.

Extreme care should be taken when preparing the herbicide impregnated plugs. Since the herbicide was used in undiluted form. Protection is necessary for the entire body, particularly hands and eyes. When plugs are used in the field in the wet state full protection is also required but there is less danger than for a spray or painted application. Protection for hands may only be necessary for application of dry plugs.

This technique was found to be very successful in controlling large vines of C. vitalba. There was no obvious damage to supporting vegetation and this is would allow this technique to be used safely in reserves. Application was quick and relatively easy with one person to drill the holes and another to insert the plugs. With dry plugs the process would be even faster. The herbicides most suitable for use would be picloram or picloram-2,4,5-T mixtures.

CHAPTER 8

CONCLUSION

C. vitalba has become widespread in central New Zealand. Unless prevented it is likely that it will spread into susceptible areas not yet affected. The best method of control is prevention. To distinguish areas at risk to invasion by C. vitalba it was necessary to determine factors influencing its distribution. This information can be used to protect susceptible areas and also to time the use of control measures to vulnerable stages in its life cycle.

The development of C. vitalba from seed to flowering plant may only take a year under favorable conditions. Plants grown in the glasshouse flowered after 12 months growth. Observations suggest that C. vitalba flowers only when exposed to high PPFD. Since strong wind is needed to lever fruit from the receptacle exposure to wind is important for dispersal (Sitte, 1974). Sites exposed to high PPFD also tend to be those most exposed to wind. Seeds are usually dispersed in late August and early September during strong north-westerly winds. By early September seeds were found to have satisfied their over-winter chilling requirement.

The first priority of established vines of C. vitalba in spring is to undergo a rapid growth phase. Bud burst occurs in early August before most European tree species. This would allow establishment of C. vitalba vines before bud burst in other species. In December flowering begins and lasts until April. Fruit set is reduced as temperatures drop. Seeds remain attached to the adult plant during ripening. To ripen, seeds require a period of winter chilling, The length of this possibly varies depending on frost occurrence. Seeds were found to germinate in the laboratory in early September and this coincides with the time of dispersal. Observations suggest that germination

occurs soon after dispersal as small seedlings were found in the field in early October. Germination in early spring would allow establishment of a root system before the seedling is subjected to summer drought.

Seeds have a light requirement for germination but are inhibited by exposure to long days. Total germination in the lab was higher in seeds exposed to light breaks. Shading of seeds resulted in faster rates of germination but the total percent germination was similar to that of full light. It is suggested that the faster rate of germination in low light conditions enables seedlings to establish quickly in canopy gaps before other species establish and shade the gap. This is also suggested by the high total germination percentage that occurred after exposure to short periods of light. Short light periods may simulate sunflecks, which would signal the presence of a gap in the canopy to the seed.

Seedling establishment was affected by the moisture content of the soil. C. vitalba was found in both glasshouse and field experiments to prefer a well drained soil. This agrees with the observations of Salisbury (1921) and Sankey (1966) that the distribution of C. vitalba is affected more by soil physical factors than by pH or the soil calcium status. In the moist climate of England, C. vitalba is found on calcareous soils which tend to have better drainage. As a result C. vitalba was classified as a calcicole species. In Continental Europe C. vitalba has a more widespread distribution (Salisbury, 1921). There was no response by seedlings of C. vitalba to calcium which was added to soils from different forest types. The apparent requirement for calcium is more likely to be due to a requirement for well drained soils.

Some forest types are more commonly infested with C. vitalba than others. The experiment measuring growth of C. vitalba on soils from different vegetation types suggested that variation in soil factors may be involved. It was found that seedlings grew faster in soils from podocarp and podocarp-broadleaf forests. Growth was significantly slower on soil from the beech forest although the soil parent material was similar for the podocarp and beech

forest soils. Addition of phosphorus to the beech soil significantly improved growth indicating that phosphorus was limiting growth in this soil. Beech forest soils tend to be low in fertility due to the slow breakdown of the leaf litter. Addition of phosphorus to the broadleaf soil resulted in a reduction of growth suggesting that other major nutrients had become limiting or that phosphorus was present at super-optimal levels. These results suggest that C. vitalba requires a fertile soil and podocarp forests tend to have fertile soils making them particularly susceptible. Most of the lowland podocarp forests which still exist are small in area and have relatively extensive margins. This makes them susceptible to frequent disturbance particularly from windthrow and grazing by stock. This opens up areas into which weed species including C. vitalba can invade.

Invasion of a forest from under the canopy requires tolerance to shade. Observations have suggested that C. vitalba is not shade tolerant and can only establish where the canopy is interrupted. Most seedlings of C. vitalba at the Kaikoura field sites were found growing around forest margins or in canopy gaps. In this study experiments with seedlings growing in differing depths of shade support these observations. At low levels of shading (45% of total PPFD) C. vitalba maintained its biomass production. Further shading (22% total PPFD) induced morphological changes in leaf structure and reduced root weight. The reduction in root weight was possibly due to the reduced evapo-transpirational demand due to the shaded conditions. Total plant biomass was reduced at 14% of total PPFD. Since the light environment under a canopy was found to be less than 15% total PPFD it is unlikely that C. vitalba seedlings would survive under an intact forest canopy. This conclusion was supported by the transplant experiment. It was found when seedlings were transplanted into different forest types that the major factor influencing their survival was the PPFD received by the site. Seedling survival was highest in the disturbed sites where the canopy was sparse.

Gas exchange measurements made on adult vines of C. vitalba gave some indication of why this species grows

poorly in the shade. Stomatal conductance and assimilation were found to saturate at relatively high PPFD around 1500-2000 $\mu molm^{-2}s^{-1}$. Full stomatal opening in C. vitalba took 20 minutes to complete after transfer from shaded conditions to full light. This requirement for high PPFD and slow opening response of stomata would prevent plants which were growing in the shade from taking advantage of short periods of high PPFD. The stomata of C. vitalba had a strong closing response to increasing VPD. This is characteristic of sun adapted plants from arid environments and is a means of controlling water loss. To survive under a forest canopy C. vitalba would have to be able to respond rapidly to sunflecks. Since sunflecks tend to be of short duration (Woodward, 1981) it would be unlikely that Clematis would survive under shaded conditions.

All this information reinforces the view that C. vitalba is a light demanding plant which can only regenerate in canopy gaps or on forest margins. The chilling requirement for seed germination indicates that it is not likely to establish well north of Auckland where winter temperatures are higher. Due to the high rainfall and waterlogged soils establishment of C. vitalba on the West Coast of the South Island is unlikely. As a result areas at greatest risk to infestation by C. vitalba are likely to be small areas of forest on fertile, well drained soils. These forest remnants are more susceptible to disturbance by natural and human activities. If the remnant can be protected from canopy damage, C. vitalba is unlikely to become established except around the edges.

Control

When C. vitalba is already established in a forest area, some control method which does not injure native vegetation is required. The use of wooden plugs impregnated with 2,4,5-T and picloram inserted into holes drilled into mature stems killed vines without damaging surrounding vegetation. Other similar methods such as injecting herbicide solutions or pastes may also be effective and require further study. The wooden plug method was found to be a quick, easy and effective method to use without damage

to supporting vegetation.

Spread of C. vitalba from gardens has resulted in the infestation of nearby reserves. This will continue unless some means of determent is enforced, particularly in at risk areas where C. vitalba is not yet a problem. The most effective means of controlling weeds such as C. vitalba is to prevent their further spread.

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APPENDIX 1

EQUIPMENT

PPFD Light Measurements
LI-COR LI-185A Light Meter with Quantum Sensor,
LI-COR Incorporated,
Lincoln, Nebraska, U.S.A..

LI-COR LI-550 Intergrating Light Meter with Quantum Sensor,
LI-COR Incorporated.

Infra Red Gas Analysis and Porometer
LI-COR LI-6000 Portable Photosynthesis System,
LI-COR Incorporated.

Leaf Area
LI-COR LI-3100 Leaf Area Meter,
LI-COR Incorporated.

Delta-T Area Meter,
Delta-T Instruments, Cambridge, U.K..

PMS Pressure Bomb (Model 600),
PMS Instrument Co., Corvallis,
Oregon, U.S.A..

APPENDIX 2

CONTROLLED ENVIRONMENT CONDITIONS

Glasshouse

Temperature was maintained at 22 C day and 15 C night by an evaporative cooling system and heat pumps.

Watering was by an automatic overhead watering system controlled by an Irritrol MC-8 controller.

Summer conditions. Automatic watering was used for periods of 2 minutes four times daily from October to mid-March.

Winter Conditions. Day extension lighting using high pressure sodium discharge lighting was used during winter. Lights were used from March to September from 4-30pm to 9-30pm.

Automatic watering was reduced to periods of 2 minutes two times daily from mid-March to September.

APPENDIX 3

NUTRIENT SOLUTIONS

Complete Nutrient Solution (2 litres) (Tucker, 1978)

1.0 M	$Ca(NO_3)_2.4H_2O$	10ml
1.0 M	KNO_3	10ml
1.0 M	$MgSO_4.7H_2O$	4ml
1.0 M	KH_2PO_4	2ml

Micronutrients (Bold, 1965)

1. EDTA 50g/l and KOH 31g/l
2. $FeSO_4$ 4.98g/l (acidified H_2O)
3. H_3BO_3 11.4g/l
4. In 1 litre $ZnSO_4.7H_2O$ 8.82g; *$KMnO_4$ 1.15g; MoO_3 0.71g; $CuSO_4.5H_2O$ 1.57g; $Co(NO_3)_2.6H_2O$ 0.49g.

*Replaces $MnCl_2.4H_2O$ which tends to form a green precipitate on standing.

Minus Calcium Nutrient Solution (2 litres)

1.0 M	KNO_3	10ml
1.0 M	$MgSO_4.7H_2O$	4ml
1.0 M	KH_2PO_4	2ml

Micronutrients as above

Acetate Buffer Stock (Dunn and Arditti, 1968)

pH= 3.6	75ml	0.1 M Na acetate
	925ml	0.1 M Acetic acid
pH= 5.6	910ml	0.1 M Na acetate
	90ml	0.1 M Acetic acid

Minus Iron Nutrient Solution

As for complete nutrient solution minus micronutrient solutions 1 and 2.

APPENDIX 4

POTTING MIX

The potting mix used in this study was mixed by volume in the ratio of 1:1:1 sand, Sphagnum moss, and bark chips. In all experiments using potting mix 1 Kgm^{-3} Osmocote (C:N:P, 15:5.2:12.5) was added to the potting mix.

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